

BIOGEOGRAPHIC, TAXONOMIC, AND CLADISTIC RELATIONSHIPS BETWEEN EAST ASIATIC AND NORTH AMERICAN *CRATAEGUS*¹

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ABSTRACT

The genus *Crataegus* possesses some 150 species, more or less, according to how apomictic complexes are treated. Two of the largest series: *Oxyacanthae* (mainly European, of about 25 species) and *Azaroli* (Mediterranean to Central Asiatic, of about 12 species) do not at first sight impinge on the topic of this paper, but their cladistic significance indicates otherwise. In temperate Asia east of about 75°E long. (through Tibet) there are some 15 species of *Crataegus* in various sections, none of which occur in North America, unless *C. scabrifolia* of Yunnan be aligned in a North American section. In North America some 100 species might be recognized in about 20 series or sections, some of which, e.g. *Cordatae*, are very distinct, one of which, *Apiifoliae*, is very similar to European *Oxyacanthae*, and another of which (sect. *Mexicanae*) is extremely like Chinese *C. scabrifolia*. Most other North American species represent a heterogeneous collection of more or less closely allied series with some apparent affinities to the *Sanguineae* of northern Asia or the Chinese and Japanese species. Cladistic analysis, using extensive outgroup comparison with other maloid genera, indicates *C. scabrifolia* (Yunnan) and *C. mexicana* to be not only among the most primitive, but also mutually similar. Their affinity with *Pyracantha* and that of other *Crataegus* with *Mespilus* indicates basal possibilities for the genus. One is thus led to postulate a primitive scabrifolioid-mexicanoid stock of warm-temperate origin that was able to cross Beringia in the early Tertiary or Miocene and migrate southward. Thence, evolution toward the extant species is most parsimoniously derived from a south China relictual base with spread into western Eurasia (one major line); eastern Asia through Beringia to a North American diversification (a minor line); and a minor North American diversification from mexicanoid stock. It should be noted that (except for modern introductions) no *Crataegus* species of North America and Eastern Asia are conspecific. Also, except for the postulated ancient relicts, no two species from the two continents are even particularly close taxonomically. The evidence suggests that *Crataegus* is an old genus, quite possibly of early Tertiary age, that spread once or twice into the Americas with two probable major diversifications and probable much late Tertiary extinction. Present-day Eurasian *Crataegus* are mainly derived from Chinese stock. Thus, while the Tertiary period permitted somewhat parallel evolution of Asian and North American *Crataegus*, except for relictual taxa, they are not very closely related.

When I was deciding what materials on the enormously fascinating and complex genus *Crataegus* might be presented for the St. Louis Systematics Symposium in 1982 I had to come to terms with how to handle incomplete work. My answer was strongly influenced by the view that *Crataegus* has received no comprehensive treatment that was both modern and effective. Therefore, this contribution, which incorporates modern findings of other workers in addition to my own, represents more than a progress report—it sets out an entire scenario. I feel, therefore, that it is no exaggeration to claim that the progress made in the systematics of *Crataegus* in recent years permits one to present a credible biogeographic analysis of the genus for the first time. This progress has included modern, floristic works

for almost the whole of the range of the genus, numerous studies on reproductive biology, e.g. introgressive situations (e.g. Byatt, 1975, 1976a; Love & Feigen, 1979), chromosome counts showing three levels of ploidy (2x, 3x, 4x) (Gladkova, 1968; Muniyamma & Phipps, 1979a; Dickinson, unpubl.; Smith, unpubl.), the cytological proof of apomixis (Muniyamma & Phipps, 1979b) and the extension of this knowledge to a number of taxa (Muniyamma & Phipps, 1984; Dickinson & Phipps, submitted; Smith & Phipps, unpubl.), knowledge of the phenetic dissection of apomictic complexes (Sinnott & Phipps, 1983; Dickinson & Phipps, submitted; Smith & Phipps, unpubl.), etc. The specific contributions of this paper will include a numerical taxonomic analysis of the genus that permits of more rational

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TABLE 1. J. C. Loudon's Classification of *Crataegus* in Arboretum et Fruticetum Britannicum (1838).

I.	Sect. <i>Coccineae</i> Loud. (p. 816) 2 species, incl. <i>C. coccinea</i> L. both with varieties
II.	Sect. <i>Punctatae</i> Loud. (p. 818) 2 species, incl. <i>C. punctata</i> Ait. (sic)
III.	Sect. <i>Macracanthae</i> Loud. (p. 819) 1 species: <i>C. macracantha</i> Lodd.
IV.	Sect. <i>Crus-galli</i> Loud. (p. 820) 3 species, incl. <i>C. crus-galli</i> L.
V.	Sect. <i>Nigrae</i> Loud. (p. 822) 2 species: <i>C. nigra</i> Waldst. & Kit. and <i>C. purpurea</i> Bosc.
VI.	Sect. <i>Douglasii</i> Loud. (p. 823) 1 species: <i>C. douglasii</i> Lindl.
VII.	Sect. <i>Flavae</i> Loud. (p. 823) 3 species, incl. <i>C. flava</i> Ait.
VIII.	Sect. <i>Apiifoliae</i> Loud. (p. 824) 1 species: <i>C. apiifolia</i> Michx. (= <i>C. marshallii</i> Egglesst.)
IX.	Sect. <i>Microcarpae</i> Loud. (p. 825) 2 species: <i>C. spathulata</i> Ell. (sic) and <i>C. cordata</i> L.f.
X.	Sect. <i>Azaroli</i> Loud. (p. 826) 5 species, incl. <i>C. azarolus</i> L.
XI.	Sect. <i>Heterophylla</i> Loud. (p. 829) 1 species: <i>C. heterophylla</i> Flugge
XII.	Sect. <i>Oxyacantha</i> Loud. (p. 829) 1 species: <i>C. oxyacantha</i> L. [= <i>C. laevigata</i> (Poir.) DC.]
XIII.	Sect. <i>Parvifoliae</i> Loud. (p. 841) 3 species, incl. <i>C. parvifolia</i> Ait. (= <i>C. uniflora</i> Muenchh.)
XIV.	Sect. <i>Mexicana</i> Loud. (p. 843) 1 species: <i>C. mexicana</i> Moc. & Sessé
XV.	Two other sections are not now included in <i>Crataegus</i>

species groupings on a world-wide basis than hitherto presented, the biogeographic analysis itself, and supportive interpretations from cladistics, dispersal biology, and to a lesser extent, considerations of paleoclimate, paleogeography and some *Crataegus* fossil evidence. It is my considered view that such a synthesis of mutually supportive data from these different viewpoints and workers is vital to disentangling a genus such as *Crataegus*, which has been called somewhat alarmingly "a veritable witches' brew."

The conditions for generating an adequate biogeographical analysis are: (a) an adequate species-list; (b) adequate range maps; (c) understanding of species' relationships within the taxa under study; (d) knowledge of dispersal biology, and (e) knowledge of these topics in times past. I consider that (a) and (b) exist to adequate standards from literature compilation, a revision of our own (Phipps & Muniyamma, 1980) and herbarium studies on many species. I will present new materials for (c) in this paper (phenetic and cla-

distic) and will use available knowledge on (d) and (e). The understanding of the dispersal biology of *Crataegus*, although sketchy, appears reliable for the arguments to be made, although paleontological data, excepting pertinent paleogeography, is sparse.

The genus *Crataegus* is taxonomically quite well-known at the regional level, although apomictic complexes, some active introgressive situations, and some relatively rare segregates from apparently older hybrid situations may complicate the picture locally. The genus is most common between 30° and 50° N latitude although some extensions north and south of these limits may be found. In spite of the abundance of species and the ecological significance of *Crataegus*, there is no really worthwhile and comprehensive treatment of this genus that has been presented hitherto. Regional floras, e.g. Franco (1968), for Europe, Maire (1980) for North Africa, Browicz (1972) for Turkey, Riedl (1969) for the Flora Iranica region, Pojarkova (1939) for the USSR, and Yü and Ku (1974) for China cover Eurasia effectively at the normal level of good floristic treatments. The remaining smaller areas in Asia possessing *Crataegus* (Levant, Korea, Japan) are also adequately covered. The floristic effort in North America has been just as great with major contributions by Palmer (e.g. 1953) and Kruschke (1965) for the Northeast and Tidestrom (1933) for the Southeast. State and regional floras for the United States west of the Mississippi, Canada, and Alaska, combine to cover all species of the western half of the United States and Canada but there is no comprehensive treatment for Mexico since Standley (1922). However, in spite of apparently complete regional coverage, there remains uncertainty about the reliability of treatments of certain species groups, especially some of those concentrated in Texas and the eastern United States. The situation undoubtedly reflects real taxonomic problems, as is now demonstrated, for instance, by the work on cytology and reproductive behaviour, on apomixis, on polyploidy, on phenetic dissection in the genus, as mentioned earlier, and is thus not an artefact of bad taxonomy. Thus, the taxonomic problems are real and almost certainly have contributed to the avoidance of a holistic study of the genus. These taxonomic difficulties can, of course, lead to some lack of precision for the biogeographical analysis because of the incommensurability of taxa of the 'same' rank and certain fuzzy species' boundaries based on taxonomic uncertainties.

TABLE 2. C. K. Schneider's classification of *Crataegus* in *Illustriertes Handbuch des Laubholzkunde* (1906). Note—authorities as attributed by Schneider are not necessarily correct. Phipps (1983) provides correct citations for serial and sectional names.

1. Sect. *Pinnatifidae* Zabel (p. 769) 3 species, incl. *C. pinnatifida* Bunge
2. Sect. *Sanguineae* Zabel (p. 771) 6 species, incl. *C. sanguinea* Pallas
3. Sect. *Douglasianae* Rehd. (p. 775) 2 species, incl. *C. douglasii* Lindl.
4. Sect. *Tomentosae* Sarg. (p. 776) 3 species, incl. *C. tomentosa* L.
5. Sect. *Pentagynae* C. K. Schneid. (p. 777) 2 species: *C. pentagyna* Waldst. & Kit. and *C. nigra* Waldst. & Kit.
6. Sect. *Oxyacanthae* Zabel (p. 779) 5 species, incl. *C. oxyacantha* L.
7. Sect. *Orientales* Zabel (p. 786) 7 species, incl. *C. orientalis* Pallas
8. Sect. *Microcapae* Koch (p. 790) 3 species, incl. *C. apiifolia* Michx.
9. Sect. *Brevispinae* Beadle (p. 791) 2 species, incl. *C. brachyacantha* Engelm. & Sarg.
10. Sect. *Flavae* Sarg. (p. 792) 2 species, incl. *C. flava* Ait.
11. Sect. *Uniflorae* Beadle (p. 793) 1 species: *C. uniflora* Muenchh.
12. Sect. *Cuneatae* Rehd. (p. 793) 1 species: *C. cuneata* Sieb. & Zucc.
13. Sect. *Mexicanae*, sect. provis. (p. 794) 1 species: *C. stipulosa* Steud.
14. Sect. *Aestivales* Sarg. (p. 794) 1 species: *C. aestivalis* Torr. & Gr.
15. Sect. *Punctatae* Sarg. (p. 794) 2 species, incl. *C. punctata* Jacq.
16. Sect. *Crus-galli* Sarg. (p. 796) 1 species: *C. crus-galli* L.
17. Sect. *Triflorae* Beadle (p. 797) 1 species: *C. triflora* Chapm.
18. Sect. *Molles* Sarg. (p. 797) 2 species, incl. *C. mollis* Scheele
19. Sect. *Virides* Sarg. (p. 798) 2 species, incl. *C. viridis* L.
20. Sect. *Pruinosae* Sarg. (p. 798) 1 species: *C. pruinosa* K. Koch
21. Sect. *Coccineae* Sarg. (p. 799) 4 species, incl. *C. coccinea* L.
22. Sect. *Intricatae* Sarg. (p. 801) 3 species, incl. *C. intricata* Lange

TABLE 3. Series of the genus *Crataegus* as proposed by Rusanov (1965) in *Dendrologii Uzbekistanii* (from Cinovskis, 1971).

Ser. 1. <i>Pinnatifidae</i>	Ser. 14. <i>Macracanthae</i>
Ser. 2. <i>Henrianae</i> (sic)	Ser. 15. <i>Punctatae</i>
Ser. 3. <i>Microcarpae</i>	Ser. 16. <i>Rotundifoliae</i>
Ser. 4. <i>Oxyacanthae</i>	Ser. 17. <i>Intricatae</i>
Ser. 5. <i>Nigrae</i>	Ser. 18. <i>Brainerdianae</i>
Ser. 6. <i>Pentagynae</i>	Ser. 19. <i>Cordatae</i>
Ser. 7. <i>Douglasianae</i>	Ser. 20. <i>Silvicolae</i>
Ser. 8. <i>Sanguineae</i>	Ser. 21. <i>Pruinosae</i>
Ser. 9. <i>Calpodendra</i>	Ser. 22. <i>Molles</i>
Ser. 10. <i>Virides</i>	Ser. 23. <i>Dilatatae</i>
Ser. 11. <i>Cuneatae</i>	Ser. 24. <i>Coccineae</i>
Ser. 12. <i>Mexicanae</i>	Ser. 25. <i>Tenuifoliae</i>
Ser. 13. <i>Crus-galli</i>	

through, for instance, the work of C. K. Schneider (1906), whose classification is presented in Table 2, Sargent (1902, 1903), Palmer (1953), Kruschke (1965), Rehder (1940), Rusanov (1965—see Table 3), Cinovskis (1971), and others. These treatments vary in the geographical region covered, Kruschke and Palmer being North American, Pojarkova Russian, and the others world-wide. They also vary in the predominant rank used (Section, Series, 'natural group' or 'group'—German 'Gruppe') and the number of species known to and accepted by the author. But what these classifications have in common is "flatness." Neither Loudon's 14 sections nor Rusanov's 25 series claim any further hierarchical groupings or interrelationships. Thus, the established view of *Crataegus* taxonomy, that of many small species groups, represented the most that taxonomists would venture for some 140 years.

However, Cinovskis (1971: 19), in *Crataegi Baltici*, presented a remarkably complex reticulate set of interrelationships (Fig. 1) that, although possibly close to the botanists' dream of *Crataegus*, is very confusing and not scientifically very realistic. At the other extreme, El-Gazaar (1980) attempted to cut the Gordian Knot by erecting two sub-genera (Fig. 2), on the basis of differential leaf-shape, geographical distribution, and base chromosome number. Whereas sub-genus *Crataegus* represents, more or less, on his criteria, two related sections (*Oxyacanthae* and *Azaroli*) it is not, as he claims, restricted to Eurasia (note *C. marshallii* in the United States). His other group, "*Americanae*," purports to represent the remainder of *Crataegus*. However, the remainder of *Crataegus* is much more variable

The state of current taxonomy may be briefly reviewed here. Loudon (1838) grouped *Crataegus* into 14 sections (Table 1) of similar species. In doing so, he presented the standard format for *Crataegus* classification that has persisted

CINOVSKIS' (1971) SCHEME OF EVOLUTIONARY RELATIONSHIPS IN *CRATAEGUS*.

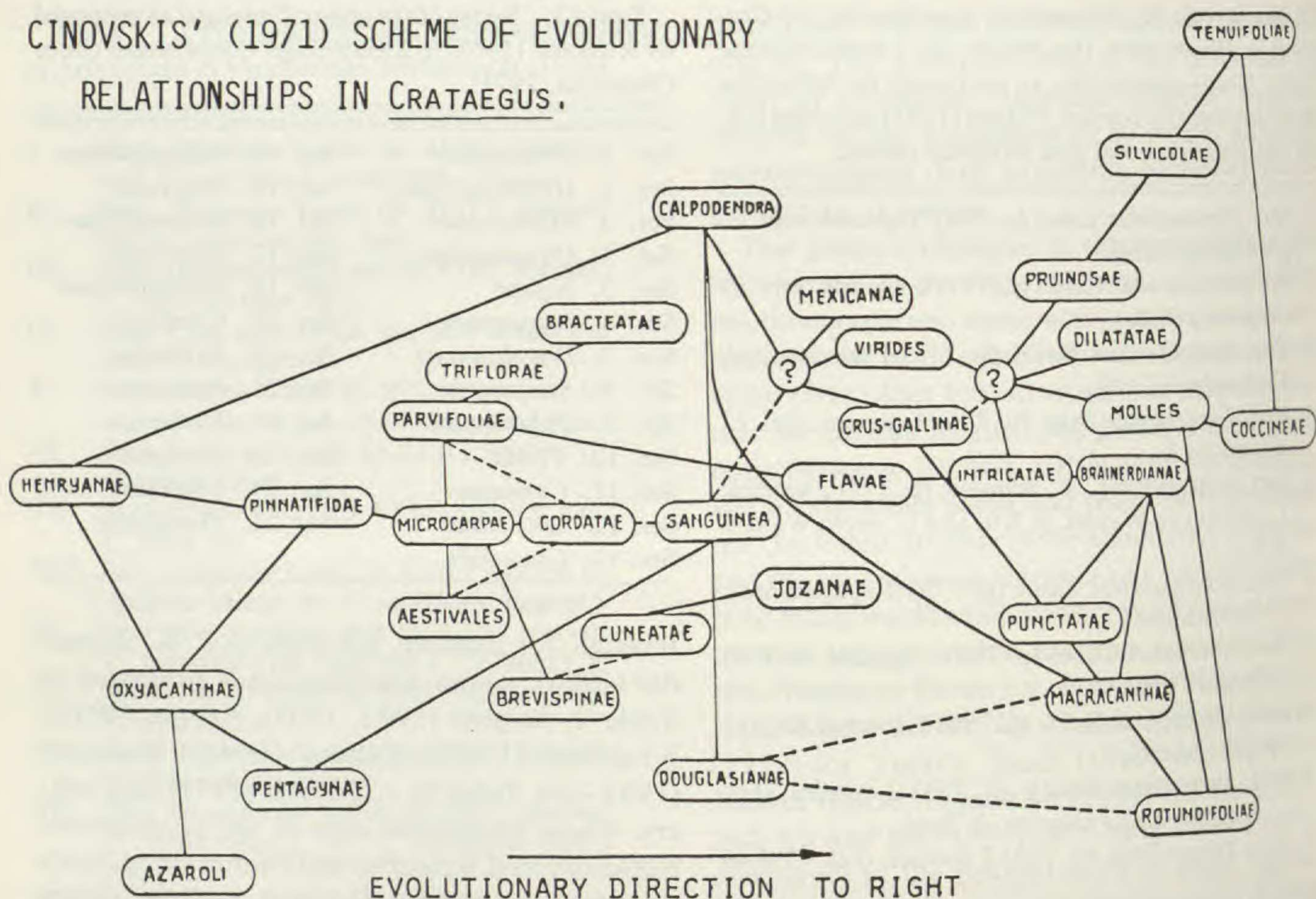


FIGURE 1. Cinovskis' (1971) scheme of evolutionary relationships in *Crataegus*.

in leaf morphology than this simple division implies, "*Americanae*"-type leaf morphology characterising most east Asian species whereas, in quoting Longley's (1924) paper based on hand-sectioned material, El-Gazaar and Badawi (1977) resurrected the totally discredited notion of $x = 16$ for North American species. El-Gazaar, regrettably, did little more than reinforce a notion already well understood by Sargent, Schneider, and others that a distinct "Oxyacanthoid" (small leaf, deeply lobed) leaf shape existed, and from there went on to totally misleading suppositions.

Thus, prior to the work to be presented here, no credible set of interrelationships within *Crataegus* has been proposed.

MATERIALS

Some 145 species of *Crataegus* are held to exist (Appendix A) and it is neither necessary nor convenient to use all for this study. For the numerical taxonomic work all the species groups (e.g. sections, series) were sampled in order to be certain to include all pertinent phenetic variation. This generated a list of 75 species (identified in Appendix A), some quite narrowly defined. This

same set of species is also used for the cladistic study.

However, because of the title of the St. Louis Symposium, the suite of taxa used in the detailed biogeographic analysis for this paper excludes the 20–25 *Oxyacanthae* and the ten or so *Azaroli* of Western Asia, Europe, and North Africa and the few small sections unique to this region. The westward demarcation line for the study is 75°E longitude. The 62 taxa used in the biogeographic study include essentially all eastern Asian (*sensu* this paper) and North American *Crataegus*. Although using a relatively complete set for the biogeographical study, somewhat different taxonomic criteria from those used in defining the cladistic set have had to be used in selecting the operational taxonomic units (OTUs) to be used in some cases. Specifically, where range-limits are still uncertain among taxonomically very close species, an entire series was sometimes used as an OTU. The lack of consistency among taxonomic rank of OTUs might concern the nominalistically inclined, but in actual fact is unavoidable.

The choice of 75°E long. western limit for eastern Asia is somewhat arbitrary. However, this

EL-GAZAAR 1977, 1980

	subgenus <i>Crataegus</i>	subgenus <i>Americanae</i>
base chr. no.	$x = 17$	$x = 16^1$
leaves	deeply incised ²	shallowly lobed ³
veins to sinuses	present	absent ³
distribution	Eurasia	North America

¹ quoting Longley, 1924 who used hand-sectioned material—correct is $x = 17$ (Moffet '31, Gladkova '68, M & Ph '79).

² Some Eurasian species have subgenus *Crataegus* foliage type.

³ Some N. American species have subgenus *Americanae* foliage type.

FIGURE 2. El-Gazaar's (1977, 1980) subdivision of *Crataegus* into two subgenera.

western study limit passing through the currently impenetrable central Asian massif of Xinjiang-Qinghai-Xijang both simultaneously and fortuitously proves to coincide with a natural taxonomic and biogeographic partition in *Crataegus*.

DATA

The morphological data used consist of 49 characters from habit, branch, thorn, leaf, inflorescence, flower, and fruit (Table 4). These are obvious *Crataegus* characters that any taxonomist would use except for the emphasis on thorn, which is underlined by this writer. All 49 characters were used for the phenetic studies. For the cladistic studies, those 18 characters that could, with adequate confidence, be polarised, were selected (Table 5). These were appropriately re-coded (see later discussion).

The biogeographical data base consists of 62 range maps. Range maps made from locality coordinates (dot maps) of individual records are by far the most sensitive, because they possess the most information content (e.g. see Phipps, 1975a) for numerical biogeographic analysis. Range maps with smooth-curve edges and no internal detail were substituted, however, because not enough dot maps are available yet. There is no problem in creating quite accurate maps from the floras mentioned, supported by more local floras, so long as consistent taxonomic decisions

are made in coordinating data from different sources and attention is paid to synonymy when grouping taxa, as discussed earlier.

PLAN OF WORK

A phenetic study using 49 morphometric characters was conducted to test what species groups existed in *Crataegus* worldwide. For this, 75 species were used, sampling all sections of the genus. The characters used are largely those conventional in *Crataegus* taxonomy, but leaf lobing and associated attributes, as emphasised already by Schneider (1906) and taken up again by El-Gazaar; and thorn type, as emphasised by this author (e.g. Phipps & Muniyamma, 1980) have more prominence than usually accorded by most workers. Due to the exceptionally large number of herbarium specimens available, median or modal values were scored. The OTUs were subjected to comparison by euclidean distance and clustered by minimum variance clustering to derive a phenogram, and to ordination by the dispersion coefficient and principal components analysis to derive a scattergram. An r-type components analysis indicated character loadings.

The biogeographical analysis depended on scoring presence-absence of species on an equiform grid of 640 km² laid on eastern Asia and North America (Figs. 3, 4). This method is somewhat crude because it does not optimize grid size

TABLE 4. Morphometric data for *Crataegus* study.*Habit:*

1. tree through small bush

Twigs:

2. color of 1-year old twigs (a)
3. color of 1-year old twigs (b)

Thorns:

4. thorns always distinct from leafy short shoots
5. modal length
6. thickness at base
7. curvature
8. frequency
9. color on 1-year old twigs (a)
10. color on 1-year old twigs (b)

Leaves:

- 11a. size: length of blade (in mm)
- b.*size: breadth at maximum point (in mm)
- 12a. shape: (char 11a/char 11b as %)
- b. shape: distance from base to widest intersect on midvein
13. shape: location of widest point: (char 12b/char 11a as %)
14. shape: angle made by base of leaf to widest point (°)
- 15a. lobing: longest lobe, measured along vein (in mm)
- b. lobing: deepest adjacent sinus (line || base of sinus to tip of lobe, in mm)
16. leaf incision index, LII (char 15b/char 15a as %)
17. number of side veins
18. leaf base—angle to widest point of blade
19. extent of lobing: (no. of lobes where LII > 20%)
20. veins to obvious sinuses: (number of where LII > 20%)
21. lobing related to vein no.: (char 20/char 19 as %)
22. pubescence above
23. glandular teeth on serration tips or petioles
24. subevergreen to deciduous

Inflorescence:

25. bracteoles at anthesis
26. number of flowers
27. pedicel indumentum
28. pedicels punctate or not

Flowers:

29. hypanthium pubescence
30. calyx: shape
31. calyx: lobe-length
32. calyx: pubescence
33. calyx: serration/lobing
34. calyx: lobes, serrae (if any), gland-tipped
35. flower diameter, cupped (mm)

TABLE 4. (Continued).

36. gynoecium: style no.
37. androecium: anther no.
38. androecium: anther length
39. androecium: anther color when fresh; (no red, pink to purple)

Fruit:

- 40a. length, excluding calyx, fresh
- b. diameter, fresh
41. diameter/length: (as %)
42. widest part: (in lower 1/3; middle 1/3; upper 1/3)
43. color when fresh and mature (yellow, red, black)
44. undamaged fruit highly pruinose
45. calyx tube (collar) present
46. calyx lobes present
47. nutlet no.
48. nutlet: strongly dorsally grooved
49. nutlet: laterally excavated

* 'b—subscripted' characters were measured, but later deleted as redundant because contributing to ratios.

as is advocated, for instance, in Phipps's "Best-block" (1975b), but the biogeographical data type (distribution maps with smooth edges) does not conveniently permit the use of such sensitive methods. Nevertheless, if the scale of grid is neither too large nor too small, pattern is still well detected. From the presence-absence data, species' arrays may be compared by positive matching coefficient and clustering to generate distribution patterns, while additive scoring of individual grid squares directly generates counts of areas of high species richness.

A cautious approach to cladistics was used in view of the high likelihood of hybrid or allopolyploid situations (e.g., Phipps, 1984). Phenetic screening of the 25 or so maloidean genera (Table 9) was conducted to identify a set of genera most closely related to *Crataegus* from which a sister-group could be generated. This set of genera constitutes the tribe *Crataegeae* Koehne. Outgroup analysis of Crataegean genera contributed to the identification of ancestral character states. Some 18 characters (subset of 49 used for the phenetic analysis) were thereby selected as confidently polarisable. A simple transform program recoded the characters with polarity. Details of the specific transforms may be found in the discussion of the cladistic results. Although available, most well-known cladistic programs that operate on a polarized character matrix were not used because

TABLE 5. Character selection and polarity for cladistic analysis.

Character No.	
1.	<i>OTU identifier</i>
	<i>Coded descriptors</i>
	0 = prim.; +ve and -ve numbers indicate advancement in various directions
	<i>Habit</i>
2.	tree (prim.) → small shrub (adv.)
	<i>Branches</i>
3.	thornless with sharp-tipped short shoots (prim.) → short thorns → long thorns (adv.)
	<i>Leaves</i>
4.	subevergreen (prim.) → early deciduous (adv.)
5.	multiveined (prim.) → few veined (adv.)
6.	angle of side-vein with midrib narrow (prim.) to wide (adv.)
7.	leaves unlobed (prim.) → deeply lobed (adv.)
8.	veins to leaf sinuses lacking (prim.) → present (adv.)
	<i>Inflorescence and flowers</i>
9.	pedicel indumentum dense (prim.) → glabrous (adv.)
10.	hypanthium indumentum dense (prim.) → glabrous (adv.)
11.	flowers medium in size (prim.) → very large (adv.) small (adv.)
12.	calyx lobes entire (prim.) → serrate (adv.)
13.	carpel number medium (prim.) → low (adv.) high (adv.)
14.	anthers white or cream (prim.) → purple (adv.)
15.	anther number 20 (prim.) → 10 → 5 (adv.)
	<i>Fruit</i>
16.	fruit oblate (prim.) → spherical → long (adv.)
17.	fruit large (prim.) → small (adv.)
18.	fruit yellowish (prim.) → reddish → black (adv.)
19.	nutlet dorsally smooth (prim.) → ridged (adv.)

they always generate furcations, not necessarily desirable in a group such as *Crataegus*. Instead, program PRIMO, which successively finds hypothetical taxonomic units (HTUs) (nodes) uniting most similar pairs of OTUs and HTUs, was run until patristic distances became too long according to a test criterion and were held likely to generate ambiguous or wrong results. The program also incorporates the capability of indicating putative hybrid situations where two or more alternative fusions show similar patristic distances within specified upper bounds. The result shown here is thus a pro-cladogram displayed in target diagram style, which postulates certain likely connections and proves to recapitulate the tighter phenetic groupings.

Conformable phenetic, biogeographical, and

pro-cladogram patterns are held to be strongly evidentiary of true cladistic relationships.

EXTRINSIC DATA

Long-distance dispersal potential, and thus mode of propagule dispersal, paleogeography and paleoclimate are critical to a full evolutionary understanding of a genus. These phenomena are considered in the discussion section, to the extent for which they are understood to date.

PHENETIC RESULTS

Using all 49 morphometric characters or only 14 leaf characters, very similar groupings of *Crataegus* emerge (Figs. 5–8). Coded on these diagrams are leaf glyphs (Figs. 5–8) and thorn glyphs

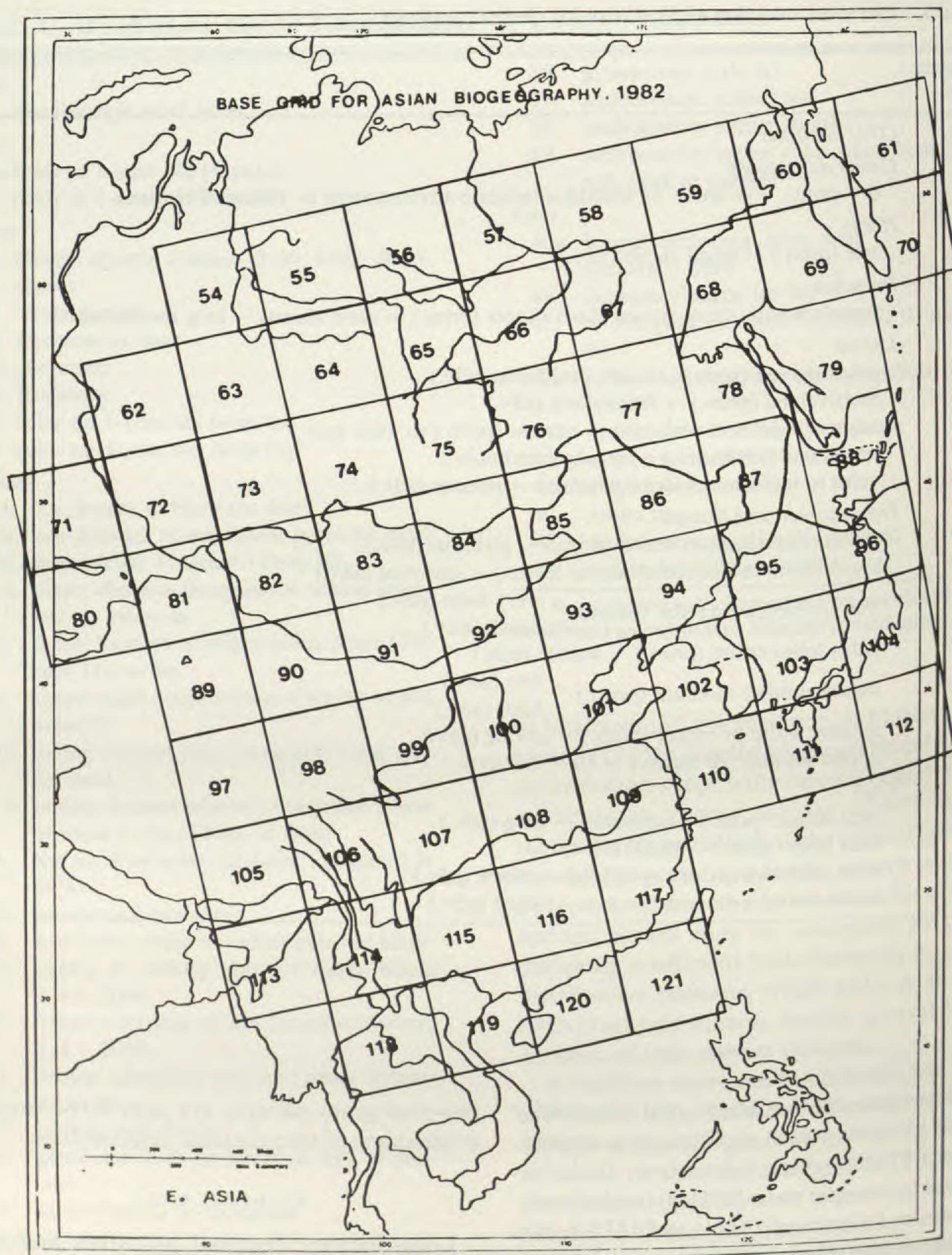


FIGURE 3. Equiform grid for eastern Asia.

(Figs. 5, 6), of which also fit well. The main groupings found are as follows:

a) Leaves narrow, multiveined, essentially unlobed:

i) with thorny short shoots: *C. mexicana*, *C. scabrifolia*

ii) with true thorns: ser. *Crus-galli*, *Punctatae*

b) Leaves usually small, broad, deeply lobed, veins to leaf sinuses:

i) with thorny short shoots: *Azaroli*, *Oxyacanthae*

ii) with true thorns e.g. *C. marshallii* (US), *C. pinnatifida* (China)

c) Trees of forest shade; fruit smallish; true thorns present; distribution SE United States:

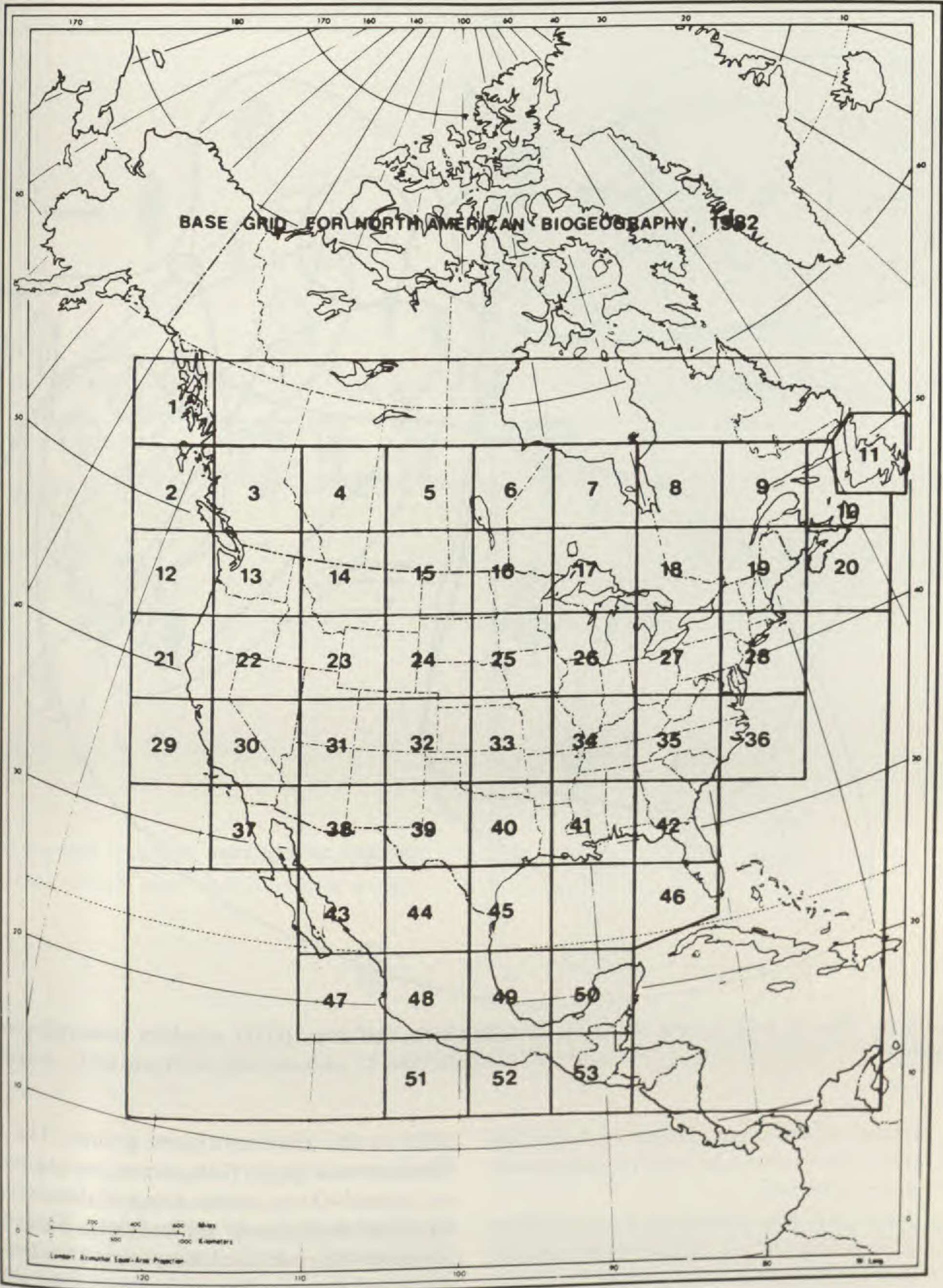


FIGURE 4. Equiform grid for North America.

- i) Leaves trilobed: sect. *Cordatae* (*C. phae-nopyrum* only)

ii) Leaves otherwise (ser. *Virides*, *Parvifo-liae*, *Brevispinae*, etc.)

d) Leaves shallowly lobed, broader, ovate, ob-
- ovate, broad-elliptic to $\pm$ deltoid; true thorns present:

i) most N. American taxa. This group cor-responds to El-Gazaar's '*Americanae*' and it will probably be well justified to erect a

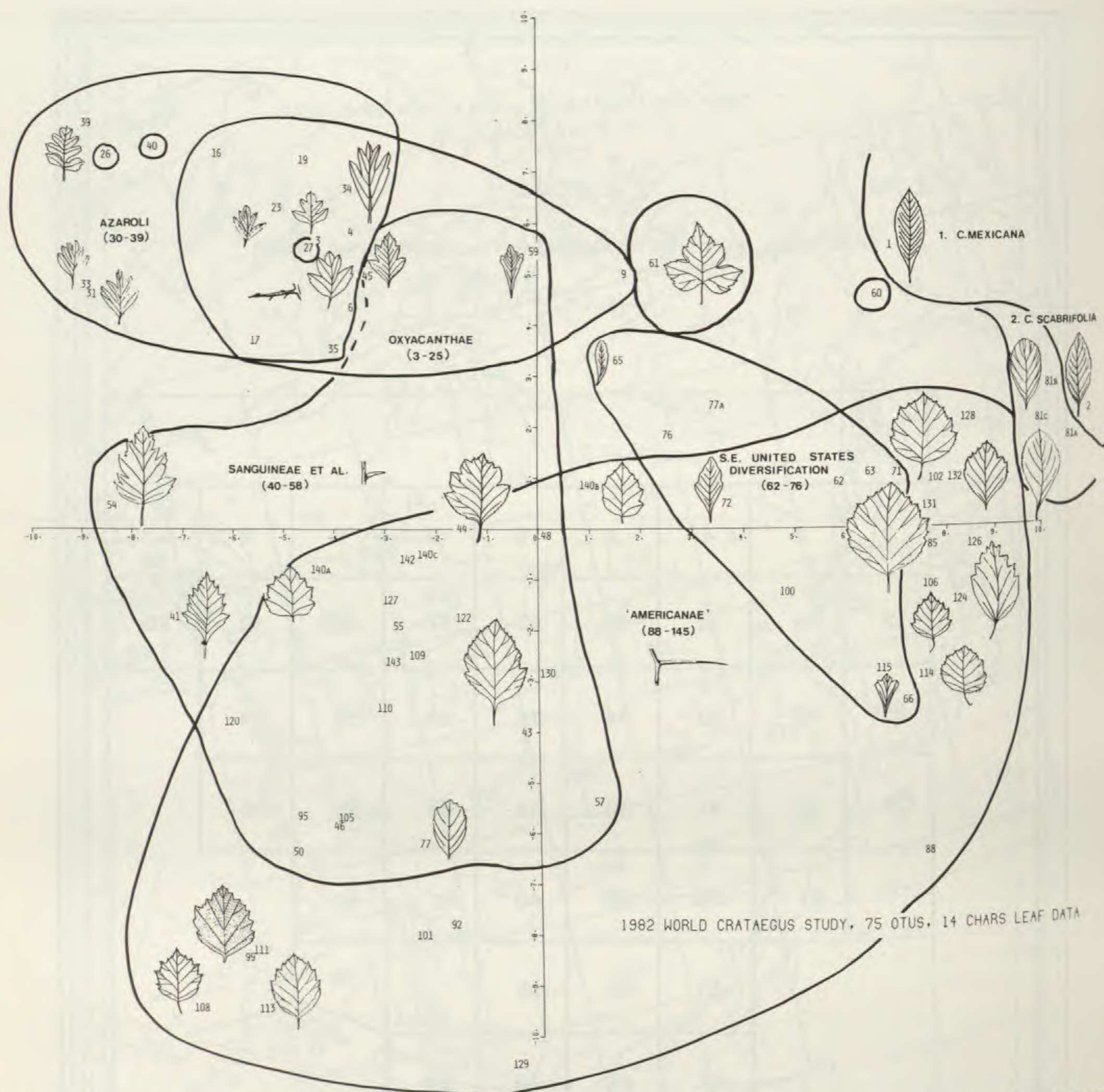


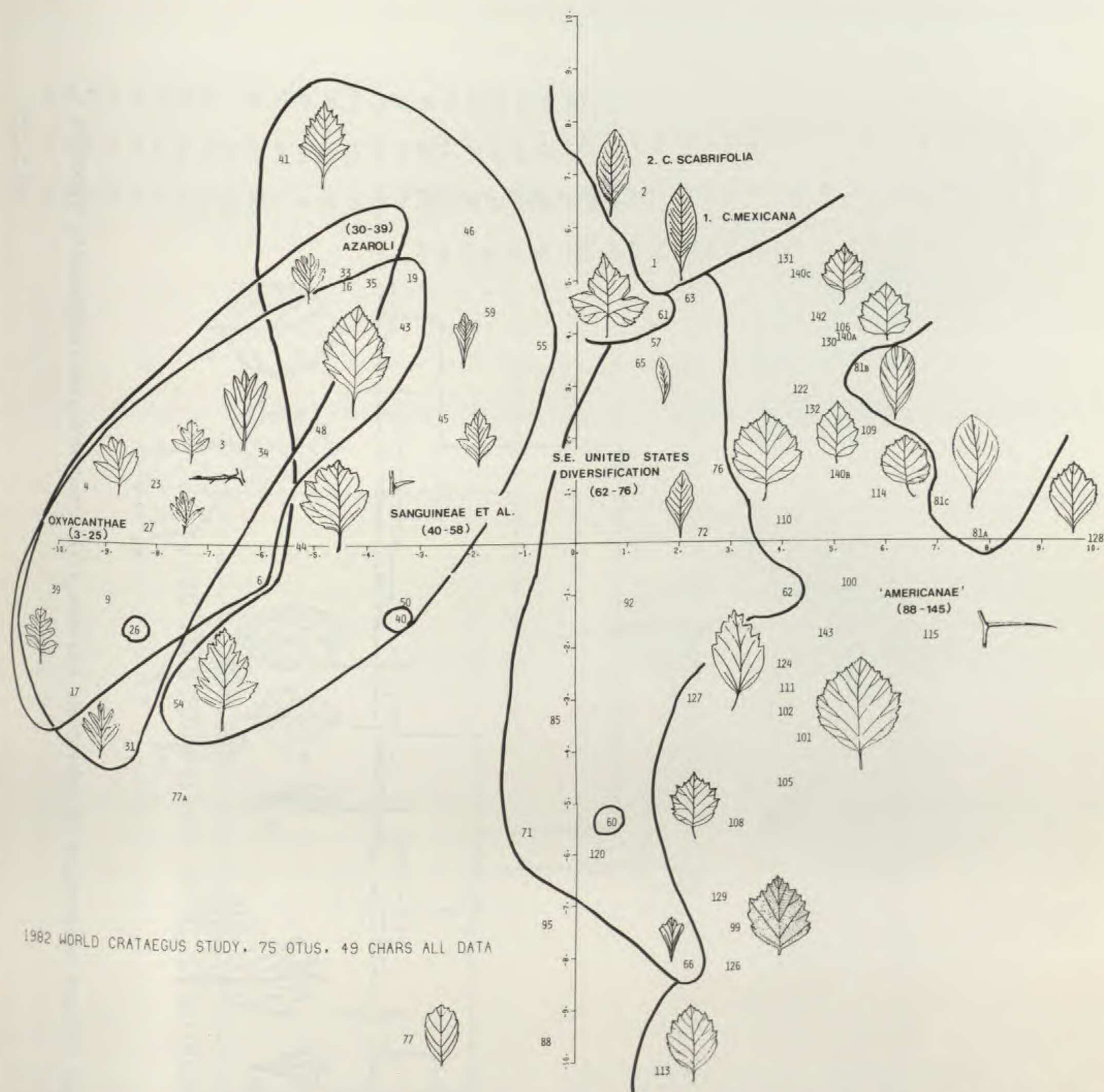
FIGURE 5. Plot of q-PCA, first two axes, 75 individuals, leaf data. (OTU numbers cross-referenced to Appendix A.)

section of this name. However, I feel that this is premature while the boundaries remain uncertain.

- ii) Some East Asian taxa (e.g. *C. kansuensis*, *C. maximowiczii*). These have shorter thorns than most 'Americanae.'
- e) Some miscellaneous leaf shapes, e.g. *C. spatulata* (US), *C. flava* (US), *C. cuneata* (China)

In the components analyses (Figs. 5 and 6) *Azaroli* and *Oxyacanthae* strongly overlap and are opposed on the first two factors by the 'Americanae' and *Crus-galli* types. Notably, *C. mexicana* and *C. scabrifolia* are closer to *Azaroli-Oxyacanthae* when all characters are considered than when leaves only are treated, when they are

polar to the aforementioned groups. The Sino-Siberian taxa (sect. *Sanguineae*, et al.) overlap the *Azaroli-Oxyacanthae* using all data but overlap only 'Americanae' on leaf data. This reflects an essentially intermediate position for the *Sanguineae*. Likewise, the southeastern United States diversification is fully overlapped by the 'Americanae' for leaves only, but has a central tendency and barely overlaps when using all data. Finally when leaves only are considered, the 'Americanae' are not only variable but almost fully overlap both the Sino-Siberian groups and the southeastern United States groups. Thus, on all counts, the *Americanae* and *Oxyacanthae-Azaroli* are the most contrasted pair, while all the other taxa are in some ways intermediate between *Americanae*



1982 WORLD CRATAEGUS STUDY. 75 OTUS. 49 CHARS ALL DATA

FIGURE 6. Plot of q-PCA, first two axes, 75 individuals, all data. (OTU numbers cross-referenced to Appendix A.)

and *Oxyacanthae-Azaroli*. This, of course, has a striking cladistic significance.

The dendrograms (Figs. 7 and 8) lend detail to the two-dimensionality of the scattergrams. Notable additional information involves the relative isolation of *C. hupehensis* and *cuneata* as well as American sect. *Flavae*. Also, the dendrogram for all data (Fig. 8) shows an interesting differentiation between more glabrous and more pubescent groups, especially in the 'Americanae.' The biological significance of this is not understood, but when it is it should aid cladistic analysis.

R-type components analyses indicate (Table 6) the very strong significance of leaf-lobing and

related characters though the loading (72%) of character 10 (pubescence) on root 3 may eventually appear to be highly significant. When considering all characters (Table 7) the major ones almost equally divide between inflorescence pubescence and related characters on the one hand and high ranking leaf characters on the other. There is clearly some broad correlation between leaf morphology and other variables indicated here which accounts for similarities in the q-PCAs and which relate to the observation in the previous paragraph.

Thus, although the presence of some intermediate taxa, together with the existence of a broad amplitude for some species groups, do not

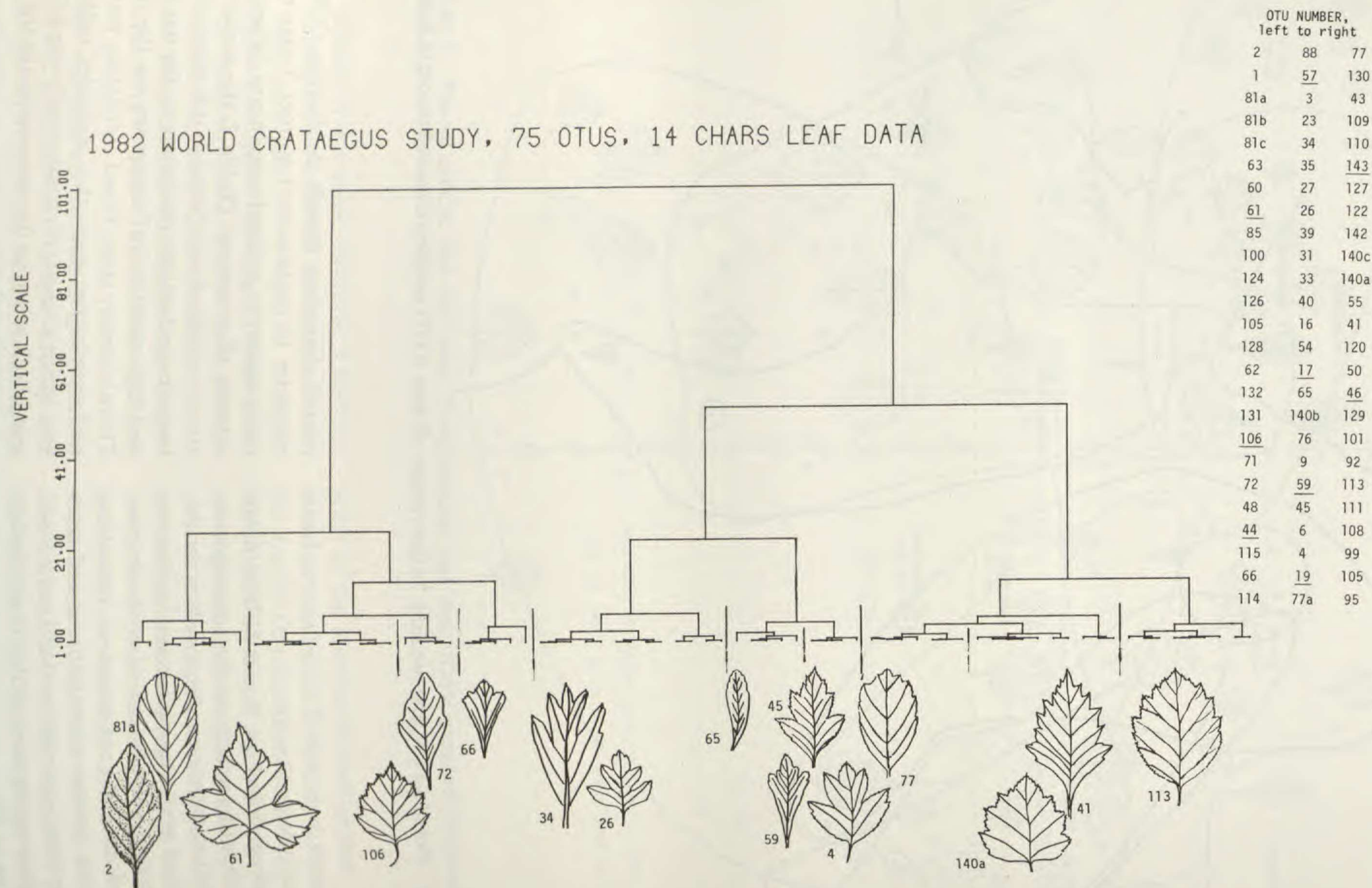


FIGURE 7. Phenogram derived from minimum variance clustering of 75 individuals, leaf data. (OTU numbers cross-referenced to Appendix A.)

OTU NUMBER,
left to right

61	6	33
132	4	43
62	77a	48
63	77	41
60	106	65
131	130	34
72	142	35
55	127	85
81a	122	71
81b	110	102
1	109	126
2	108	59
76	81c	66
57	124	129
140a	128	101
140b	115	92
140c	114	99
50	3	95
46	26	88
45	54	113
44	17	111
40	39	120
19	31	143
16	23	100
9	27	105

1982 WORLD CRATAEGUS STUDY, 75 OTUS, 49 CHARs, - ALL DATA

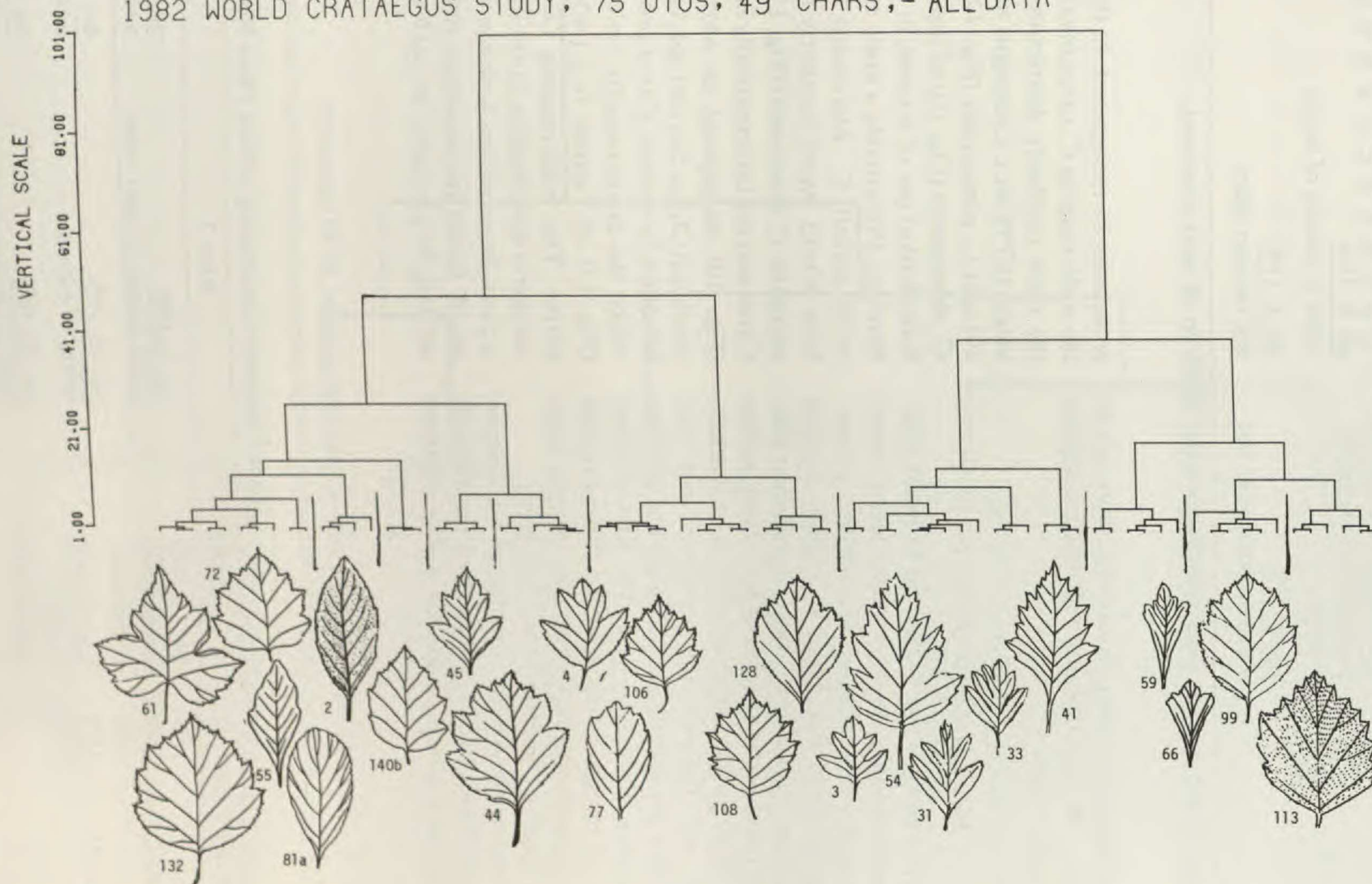


FIGURE 8. Phenogram derived from minimum variance clustering of 75 individuals, all data. (OTU numbers cross-referenced to Appendix A.)

TABLE 6. 1982 *Crataegus* study, r-type components analysis, leaf data.

Percent of Trace a/c by Each Root		Characters Contributing more than 10% Each to First Three Roots		
		Root 1	Root 2	Root 3
Root 1	32%	no. 7, 41%	no. 11, 36%	no. 10, 72%
Root 2	22%	no. of deep lobes per leaf	glandular serrations on leaf	pubescence above
Root 3	13%	no. 9, 32%	& petiole margin	
Root 4	10%	percent veins ending in	no. 8, 31%	
Roots 5-14	23%	lobes	veins to sinuses of leaves	
	100%	no. 8, 11%	no. 5, 11%	
		veins to sinuses per leaf	leaf incision index	

Character 5, leaf incision index contributes most, 10.3% on all roots combined.

generate an utterly sharp taxonomy, there can be no doubt that the taxonomic groups recognized are broadly valid.

BIOGEOGRAPHIC RESULTS

The phenogram (Fig. 9) derived from the grid-ded distributional data shows that species ranges fall strongly into readily identifiable groups. Bearing in mind that there is a slight overlap between the *Sanguineae* (e.g. *C. sanguinea* Pall. ex Bieb.) and some species of the *Oxyacanthae* and *Azaroli* in the Soviet Republics of Kazhak, Kirghiz and Tadzhik, the European and west Asian taxa are mainly very strongly cut off from those under discussion here. The first division of our phenogram necessarily differentiates Asiatic from North American taxa because there are no species common to the two areas.

Characteristic Asiatic distributions are represented in Figures 10-12. Basically a northern (N of 40°N lat.) group of species and a southern

group may be recognized. In the northern group, the wide-ranging *C. sanguinea* (Fig. 11) achieves the most northerly distribution of extant *Crataegus* (63°N lat.). *Crataegus maximowiczii* (Fig. 10) and *C. pinnatifida* (Fig. 12) of NE Asia and *C. chlorosarca* (Fig. 10) of the Pacific Rim (N to Kamchatka) are of interest in their approach to Beringia. Presumably a quite small climatic shift could permit *C. chlorosarca* to migrate to the New World. More southerly species are represented by *C. kansuensis* (Fig. 11) of north-central China and the taxonomically isolated *C. cuneata* (Fig. 10) widespread in warm temperate and southeast China. Several species of restricted distribution in western China proper are known, of which the taxonomically isolated *C. scabrifolia* (Fig. 12) of Yunnan is a particularly good example. The wide-ranging *C. aurantia*, with a northerly distribution, is not illustrated. There is a clear demarcation between northerly 'sanguineoid' forms and southern and central taxa that are largely unrelated to each other or anything

TABLE 7. 1982 *Crataegus* study, r-type components analysis, all 49 characters.

Percent Trace a/c by Each Root		Major Characters Contributing to First Three Roots		
		Root 1	Root 2	Root 3
Root 1	18%	no. 23, 30%	no. 6, 20%	no. 15, 17%
Root 2	15%	hypanthium	gland-tipping of calyx lobes	number of deep lobes
Root 3	10%	pubescence	no. 25, 16%	no. 17, 14%
Roots 4-49	58%	no. 22, 24%	lobing of calyces	lobing/vein number
	100%	pedicel	no. 16, 10%	no. 4, 12%
		indumentum	veins to obvious sinuses	color on 1-year old
		no. 18, 8%		twigs
		pubescence upper		
		side of leaves		

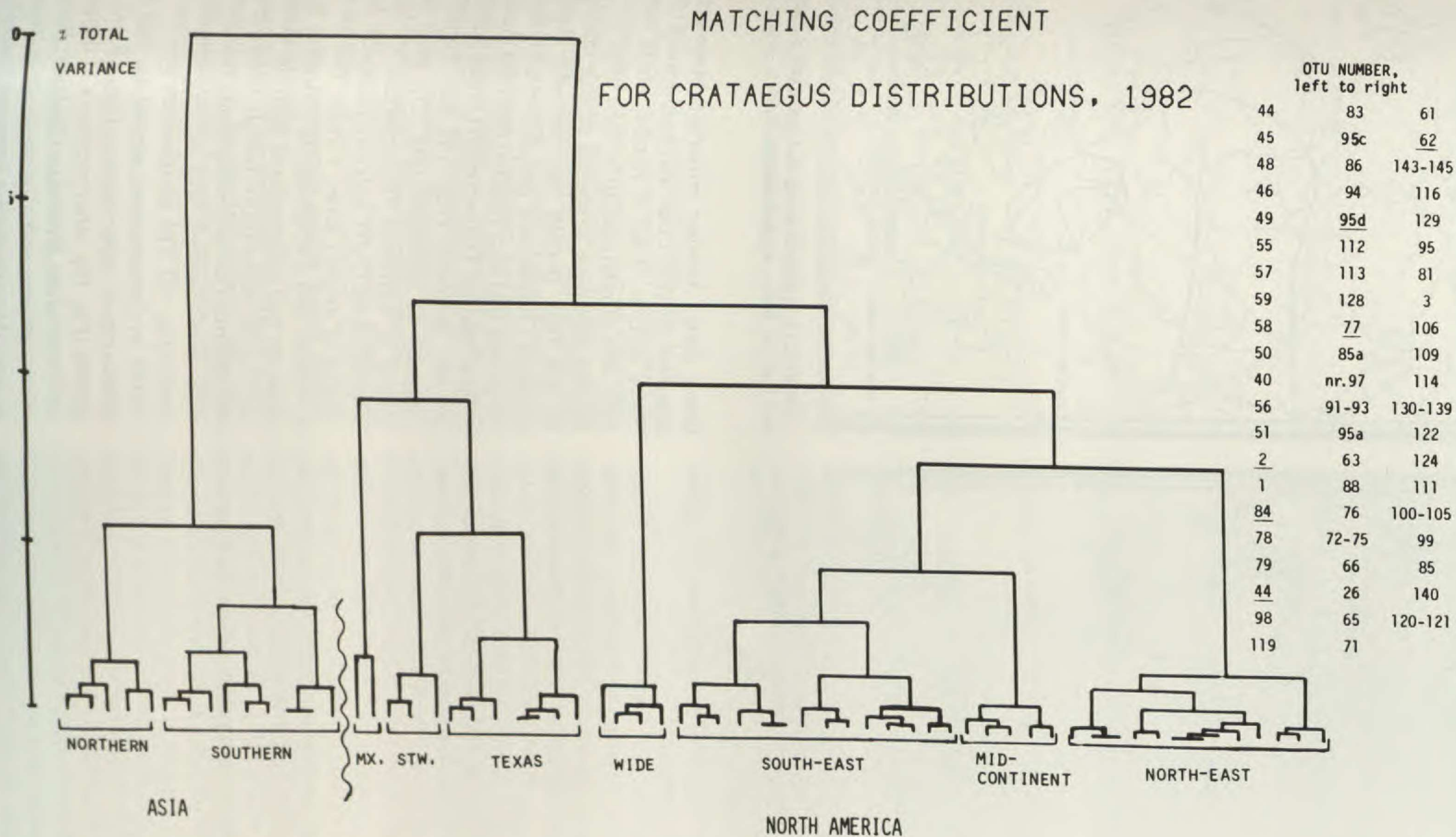


FIGURE 9. Classification of distributions derived by minimum variance clustering of positive matching coefficient. (OTU numbers cross-referenced to Appendix A.)

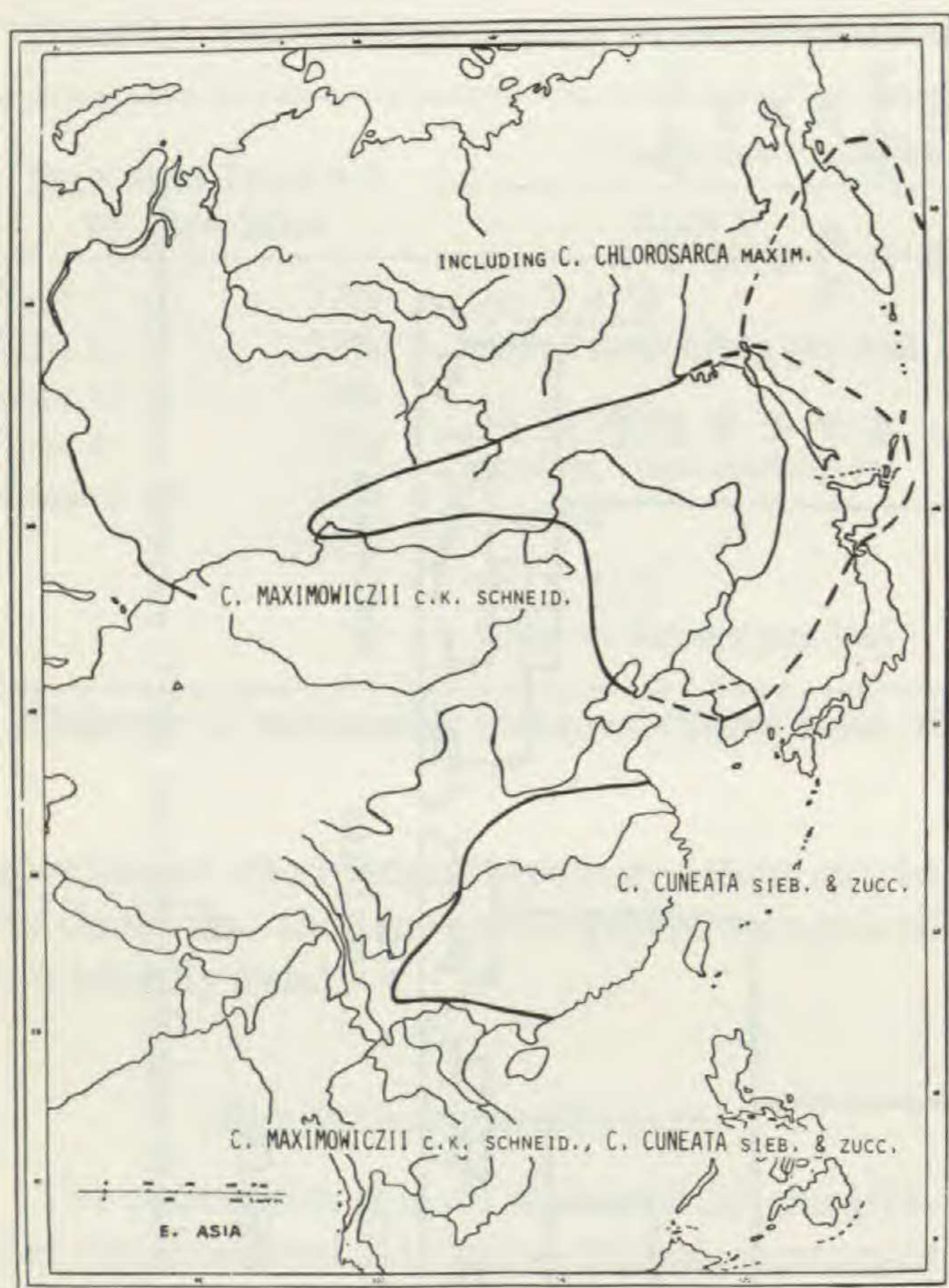


FIGURE 10. Distribution of *Crataegus*: *C. maximowiczii* C. K. Schneid., *C. cuneata* Sieb. & Zucc.

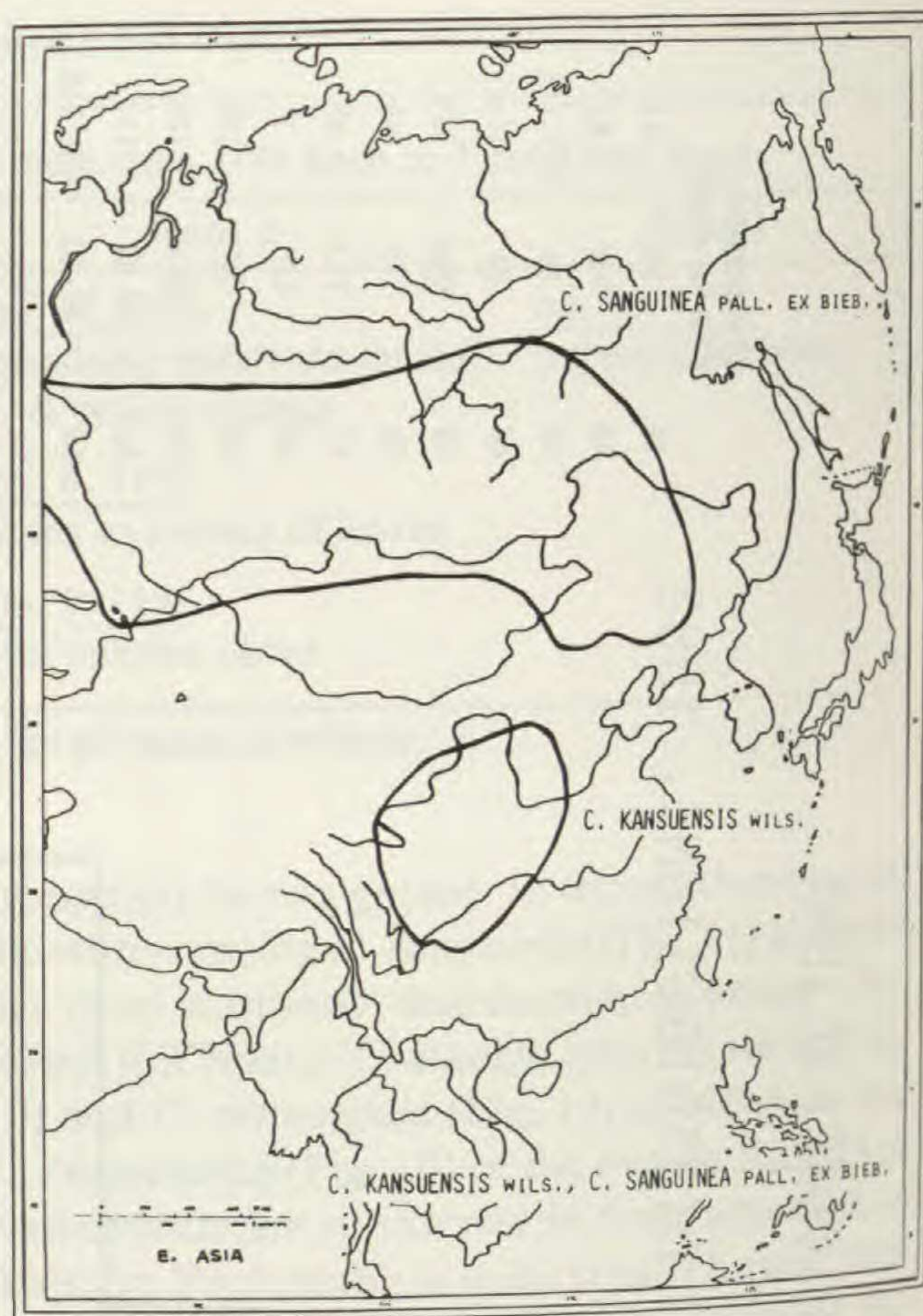


FIGURE 11. Distribution of *Crataegus*: *C. sanguinea* Pall. ex Bieb., *C. kansuensis* Wils.

else (e.g. *C. hupehensis*—not shown, *C. scabrifolia* and *C. cuneata*).

In North America, western, Mexican, Texan, southeastern, eastern, northeastern and wide ranging types stand out. There are few western species but *C. douglasii* (Fig. 13), mapped to include the possibly conspecific *C. rivularis*, is notable for its extreme northerly range extension in the Anchorage region of Alaska, remarkably near to Beringia. It should be noted that *C. douglasii* is one of the few North American species to share the short stout thorns characteristic of the sanguineoid group from Asia. *Crataegus douglasii* exhibits the migratory potential of the genus with its disjunct population around the northern Great Lakes. *Crataegus columbiana* (not mapped) would link *C. chrysocarpa* (Fig. 17) to the Pacific, if conspecific, which it is close to being. The Mexican group is dominated by the quite wide ranging *C. mexicana*, which extends through the highlands into Guatemala. It is found under similar latitudinal and climatic conditions to its closest relative, *C. scabrifolia*, of Yunnan. Texas manifests a rich variety of *Crataegus*, several of which, of quite unrelated series (e.g. *C. viburnifolia*—Molles, *C. tracyi*—*Crus-galli*) are en-

demic there. Another important biogeographic group are the Gulf Coast and southeastern United States species. What is notable about these is their lack of relationship to each other or, with the odd exception, to species outside this region. In this they parallel the mutually unrelated southern Chinese taxa (see above) and reinforce the notion that they resulted from old radiations in these regions. The pertinent United States taxa are ser. *Aestivales* (Fig. 14), ser. *Flavae* (unmapped), *C. marshallii* (Fig. 17), most closely related to European *Oxyacanthae*, *C. brachyacantha* of the Gulf Coast (not mapped), and the species of distinct series *Virides*, *Pulcherrimae*, *Cordatae*, and *Parvifoliae*. It is notable that all these are well differentiated from the northeastern United States taxa—mainly 'Americanae'—and that most are somewhat shade-tolerant small trees. Mid-continent taxa are represented by *C. mollis* (Fig. 13). The northeastern taxa are dominated by 'Americanae' species in high abundance, e.g. *C. macrosperma* (Fig. 19), *C. margaretta* (Fig. 16), other members of their series, and most of the *Silvicolae*, *Dilatatae*, *Pruinosae*, *Macracanthae*, and *Coccineae*. It is interesting to note that taxa with a large north-south range

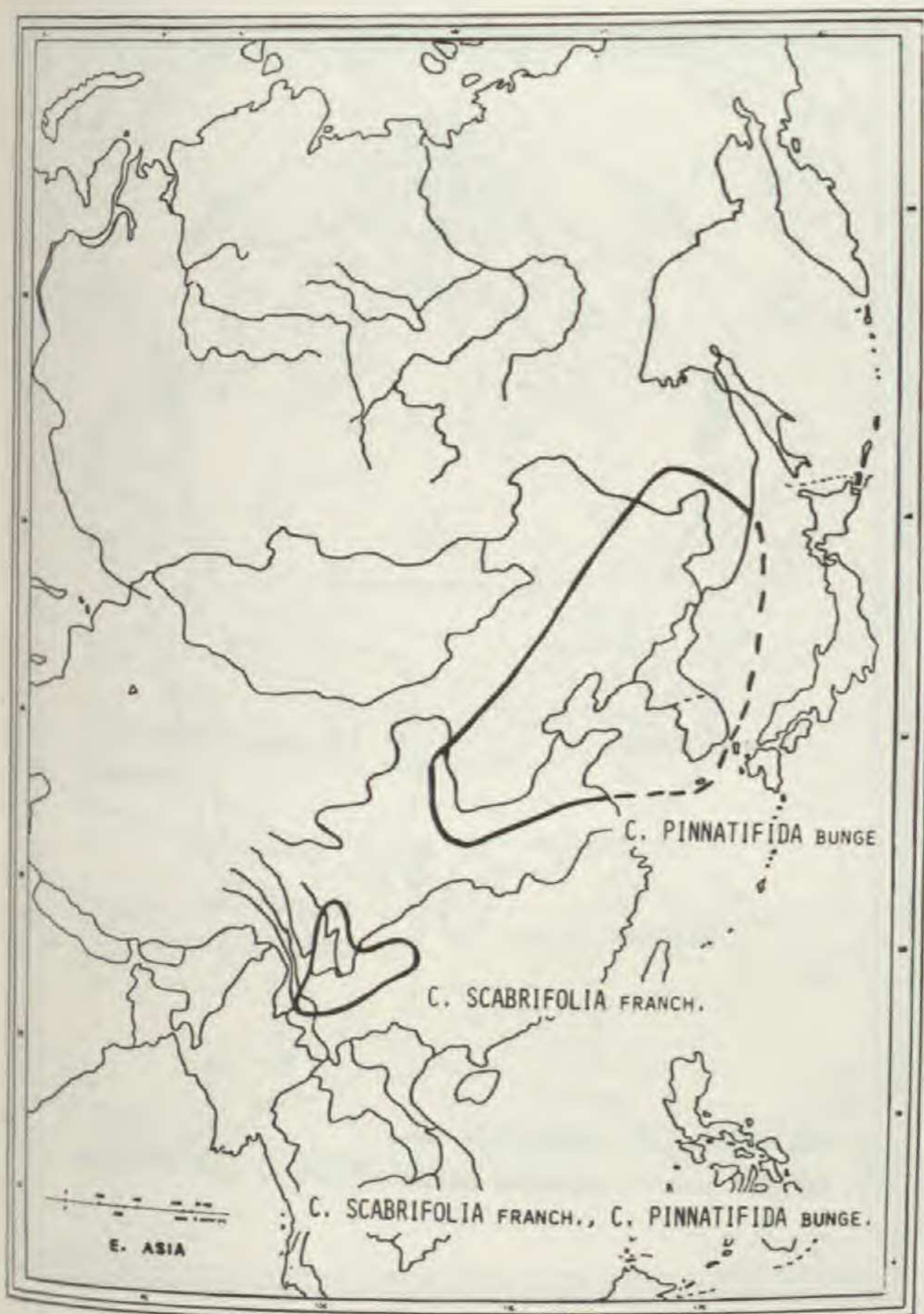


FIGURE 12. Distribution of *Crataegus*: *C. scabrifolia* Franch., *C. pinnatifida* Bunge.

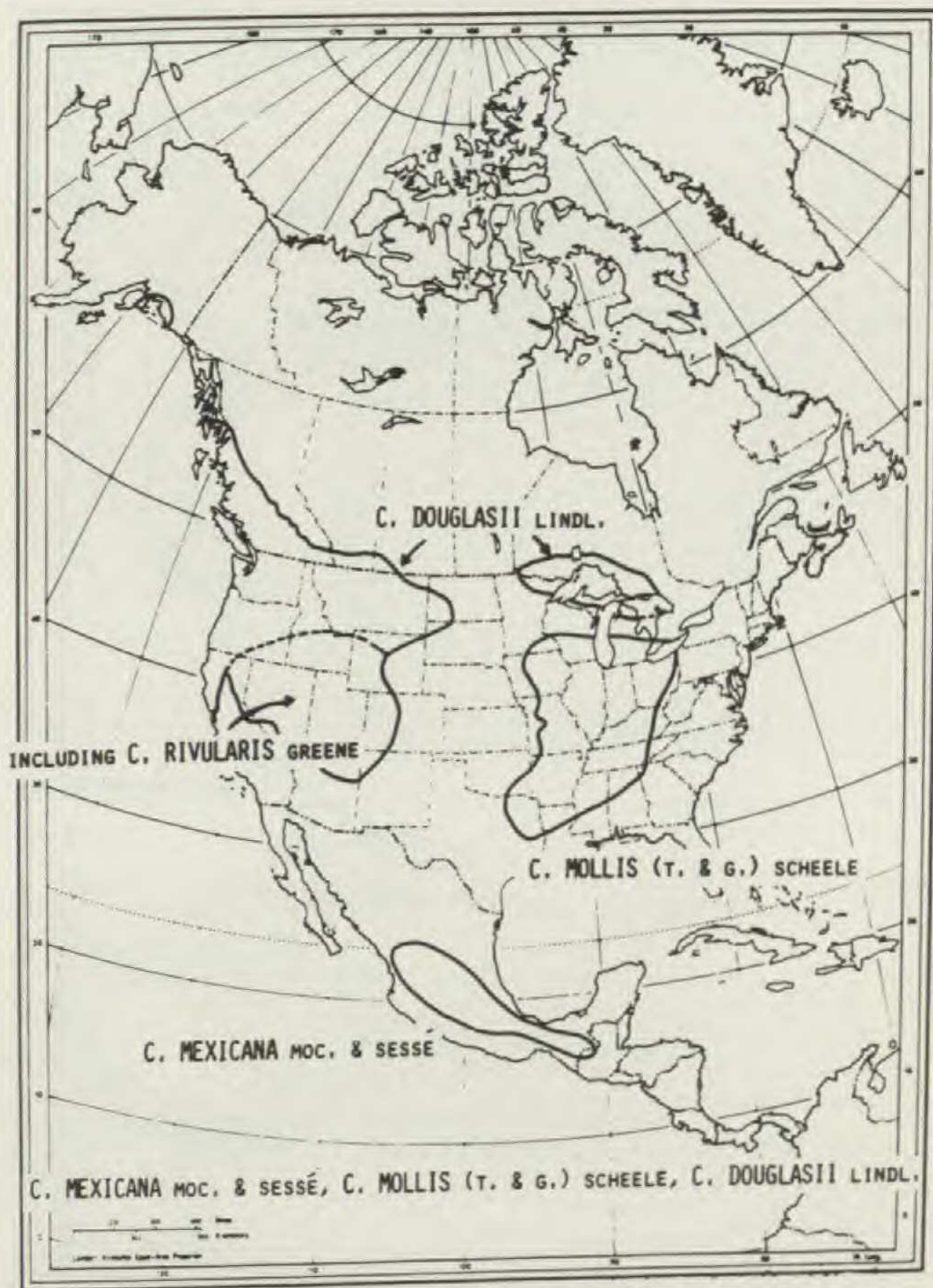


FIGURE 13. Distribution of *Crataegus*: *C. mexicana* Moc. & Sessé, *C. douglasii* Lindl., *C. mollis* (T. & G.) Scheele.

in the east, e.g. *C. crus-galli* sens. lat. (Fig. 15) and ser. *Punctatae* (*C. punctata* + *C. collina*) (Fig. 18) are neither 'Americanoid,' nor of southeastern United States relationship. Finally, some smaller series concentrated in the middle latitudes in the eastern United States must be recorded. *Bracteatae*, *Triflorae*, *Intricatae* should be noted. One of these, *C. harbisonii* (Fig. 19) is mapped and there are indications that all of these groups may represent descendants from fairly recent 'Americanae'–*Flavae* introgression. Several of the northeastern taxa range southward down the spine of the Appalachians. Even more than in Asia, taxonomic groups match biogeographical patterns.

In summary, if we consider the three major continental areas: Europe and western Asia, eastern Asia, and North America pairwise, the taxonomic relationships are as follows:

- Europe, western Asia/eastern Asia
—little similarity except slight overlap at interface
- Europe, western Asia/North America
—no similarity, except *C. marshallii*
- eastern Asia/North America

—several similarities: *Sanguineae*, *Americanae*, *C. scabrifolia*, *C. mexicana*

With regard to areas of species' richness, eastern North America as a whole stands out as far richer than eastern Asia, western North America or Mexico (Figs. 20, 21). This cannot be accounted for merely on the basis of differing taxonomic resolution of species' limits, especially because a conservative approach has frequently been made for North America by substituting single series for whole sets of species. The extreme richness of Appalachia, however, is partly an artefact of the size of grid square chosen since lowland (southeastern) species may commingle in a single grid square with predominantly northern (here mid-Appalachian) species.

The biogeographic results are rich interpretively. One notes (Fig. 21) the predominance of species in the deciduous forest biome of the Eastern United States and Europe-Russia (latter not mapped). Northward the genus may be largely delineated by the January mean -10°F isotherm, $+10^{\circ}\text{F}$ in North America (Fig. 22a, b) or, perhaps more adequately, by the southern edge of the coniferous forests. Southeastward, in two con-

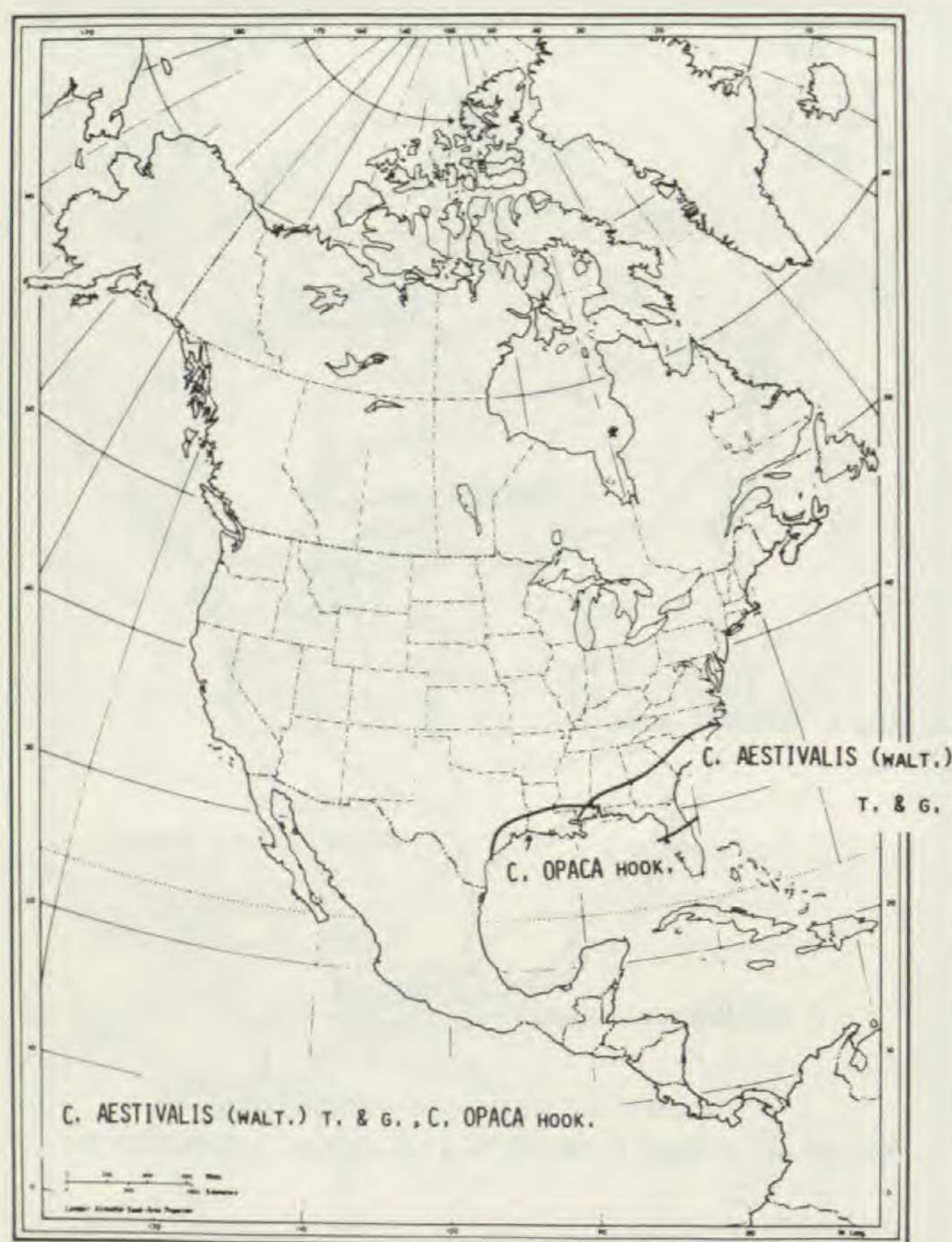


FIGURE 14. Distribution of *Crataegus*: *C. opaca* Hook., *C. aestivalis* (Walt.) T. & G. Note—encoded as *C. sect. Aestivales*.

tinents, warm climates (? mild winters) and sub-evergreen conditions appear limiting. Only one species, *C. cuneata*, occurs in southeast China (Fig. 10), and that not in Hainan, while central Florida represents the southeastern range limit for the United States. Although one is tempted to relate the southeastern continental limits of *Crataegus* to climax habitat type (trend to evergreen forest), in view of the success of other maloids in such areas (e.g. *Photinia*) this may obscure a more direct physiological relationship, perhaps that of a lack of adequate winter chilling requirements southward.

In the southeast and southern coastal plains of the United States, two ecological-adaptive groups stand out. One is the somewhat shade-tolerant tree-like group of species (e.g. *C. phaenopyrum*, *C. marshallii*, *C. viridis*, *C. brachyacantha*) of forest, often river and swamp-forest, margins, whereas the other is the more sand-plain habitat characterised by the sect. *Flavae*. It should be noted that sect. *Flavae* are trees and shrubs that appear relatively shade-intolerant like their more northern relatives. In cold, semi-arid areas (central Asia, central United States cordillera—see Figs. 20, 21, 23a, 23b) there is a virtual hiatus

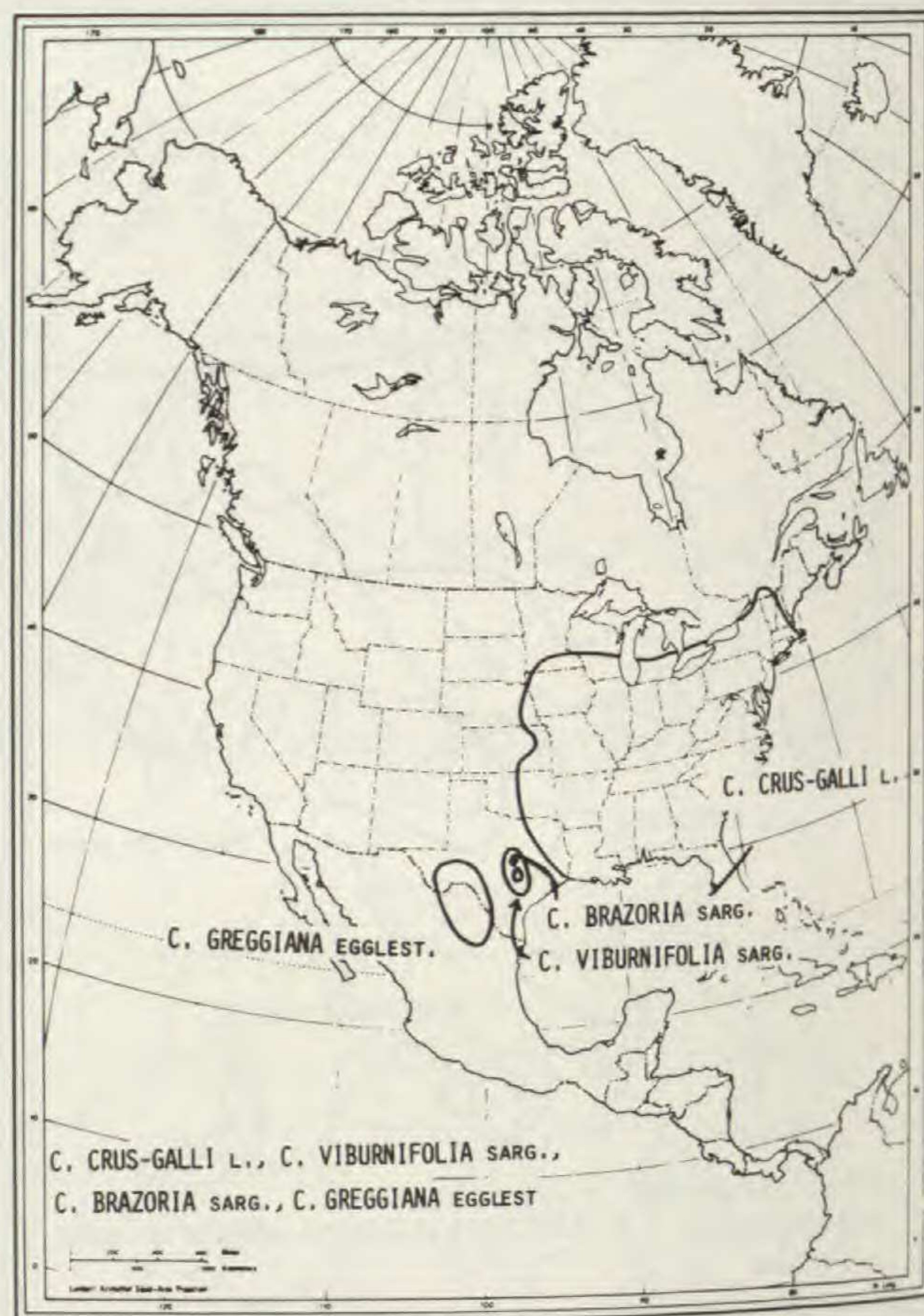


FIGURE 15. Distribution of *Crataegus*: *C. greggiana* Egglest., *C. viburnifolia* Sarg., *C. brazoria* Sarg., *C. crus-galli* L.

of *Crataegus*, indicating little success in exploiting these habitats. However, western Eurasia has developed a section (*Azaroli*) adapted to winter rainfall maxima, hot summer, scrub regions whereas no such ecological or taxonomic counterpart exists in North America. Two critical species—*C. scabrifolia* of Yunnan and *C. mexicana* of Mexico-Guatemala—are small trees, with thorns of indefinite growth, narrow, barely lobed leaves and large pink to yellow fruit. These occur in similar latitudes (about 20° to 30°N) and broadly similar climatic regions at the southern edge of *Crataegus* distribution. We will return to these apparent vicariants later.

The regions occupied by the infrageneric taxa discussed are shown on the map (Fig. 27).

CHARACTER STATE POLARITY AND OUTGROUPS

The maloids ($x = 17$) are a natural subfamily of Rosaceae whose fruit is a pome in which a fleshy hypanthial wall overlaps and often closes over the carpels during fruit development. Sterling (1964), in discussing rosaceous carpellary anatomy, agrees that *Crataegeae* are a natural



FIGURE 16. Distribution of *Crataegus*: *C. saligna* Greene, *C. margaretta* Ashe.

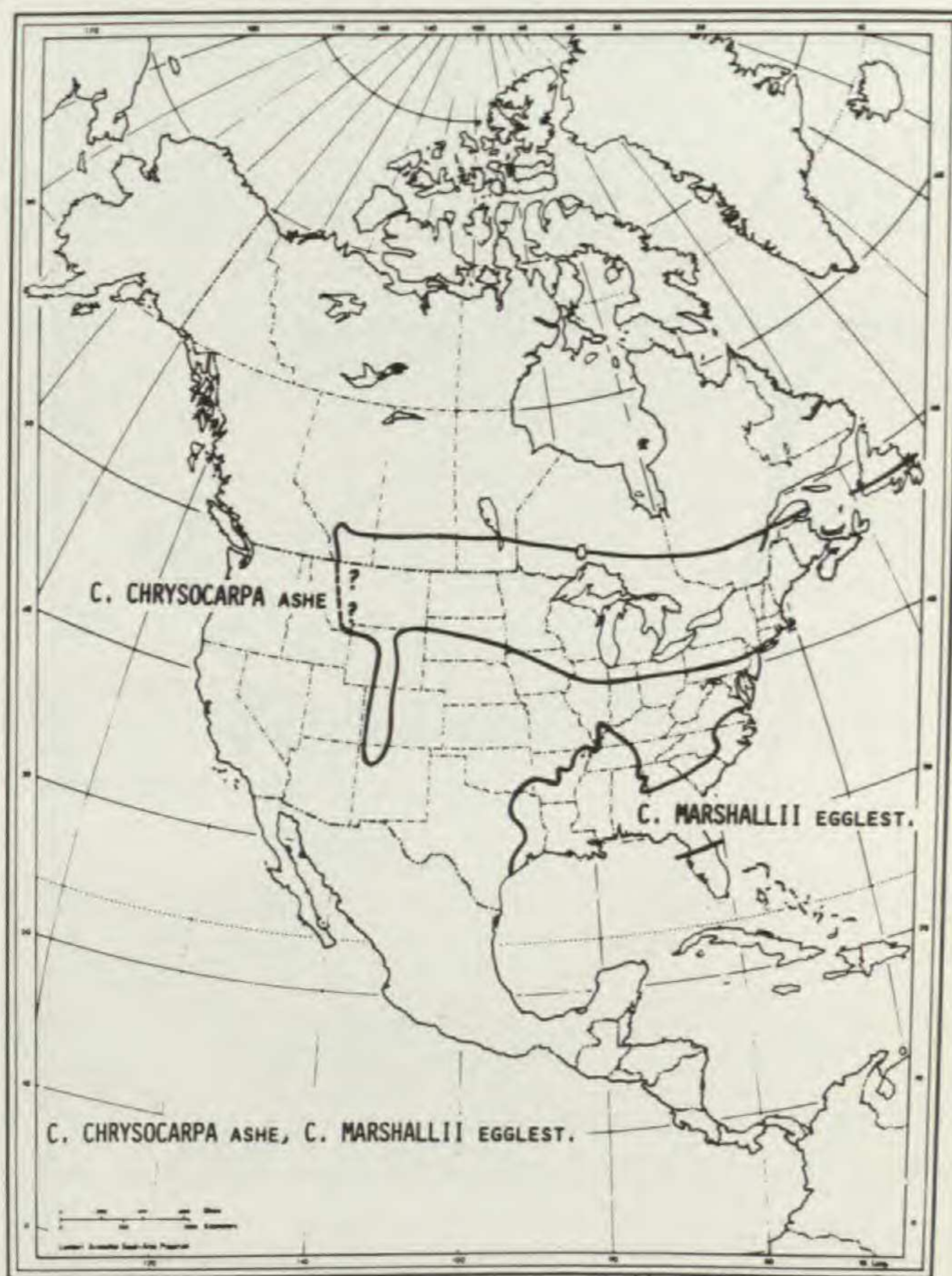


FIGURE 17. Distribution of *Crataegus*: *C. chrysoarpa* Ashe, *C. marshallii* Egglest.

group. The crataegean genera, *Crataegus*, *Pyra-cantha*, *Cotoneaster*, *Hesperomeles*, *Osteomeles*, and *Mespilus* were used for outgroup analyses.³ Crataegean characteristics (Table 8) are tendency to thorniness, small leaves, small flowers in corymbs, generally small fruit with relatively thin hypanthial wall, and bony exocarps generating pyrenes. *Mespilus* is the most distinct genus and differs strongly from other maloids in having much larger leaves and a single-flowered, large-flowered inflorescence on elongating shoots of the current season. However, it produces well-known intergeneric hybrids and a graft-chimaera with *Crataegus*, which are discussed by Byatt et al. (1977). Indeed, intergeneric hybrids are numerous in Maloideae (Fig. 24) although few of these occur in nature. Maloidean genera outside Crataegeae differ in numerous characters of habit, thorniness, evergreen-ness, gross leaf-morphology, resting bud, inflorescence (many characters), and striking characters of the development of the fruit. Mere reference to *Chaenomeles*, *Cy-*

donia, *Malus*, *Pyrus*, *Sorbus*, *Photinia*, *Amelan-chier*, *Raphiolepis*, etc. will underscore this.

It is not immediately clear, on a phenetic basis, which of the *Crataegeae* is the best genus to use as a sister group and, indeed, caution is advised due to the potential for hybridization in the subfamily and the possibility that this existed in creating ancestral *Crataegus*. The phenetic-biogeographic patterning within *Crataegus* as demonstrated earlier argues for substantially long isolation of major sections of the genus and the difficulty of Eurasian-North American migration unless evidence for widespread extinctions is verified. Indeed this is true for the Maloideae as a whole and very much so for the *Crataegeae* (Fig. 25).

The small Andean genus *Hesperomeles*, for instance, with one or two species in Costa Rica-Panama, is related to the main core of the *Crataegeae*. However, it is not very diverse and represents the only native southern hemisphere maloid. It has a specialized distribution (pygmy cloud forest and rocky outcrops at ca. 3,000 m). It is most parsimoniously derived from other *Crataegeae* as a relictual genus tenaciously holding a specialized niche but somewhat anciently crossing Beringia with a rapid move south coin-

³ *Dichotomanthes* may prove to be crataegean but has a strikingly different fruit.

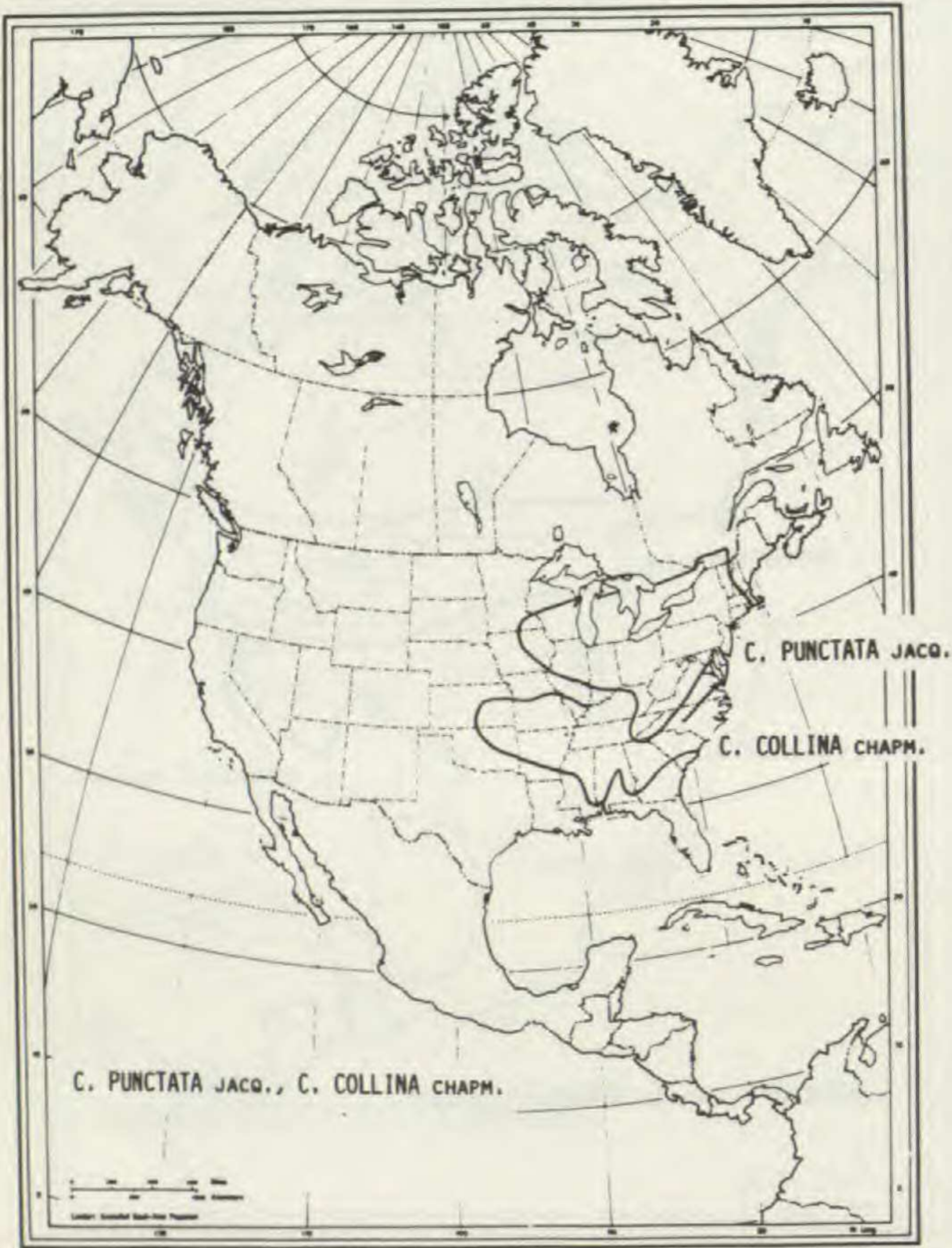


FIGURE 18. Distribution of *Crataegus*: *C. punctata* Jacq., *C. collina* Chapm.

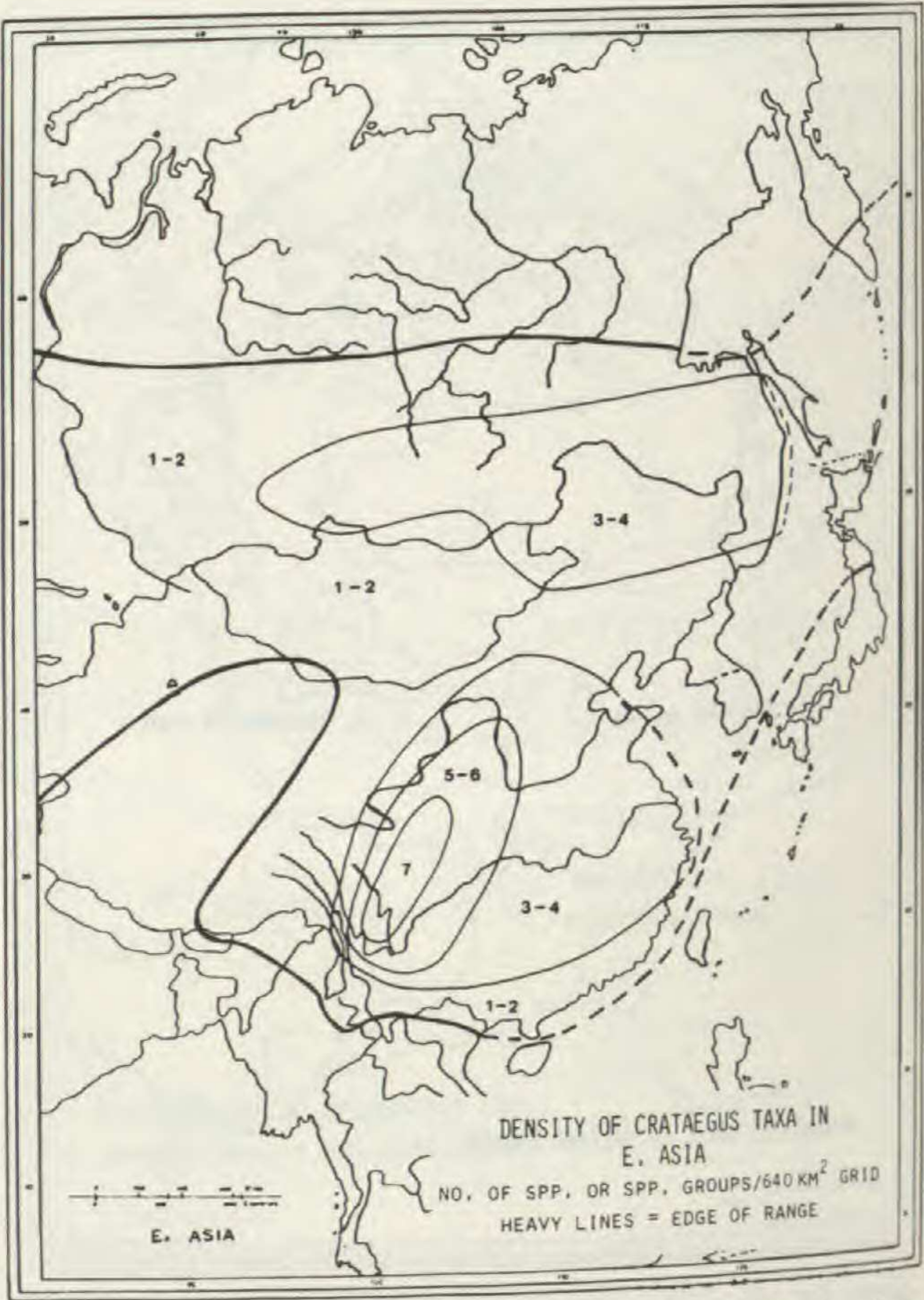


FIGURE 20. Map showing richness of species (no. per 640 km²) in eastern Asia.

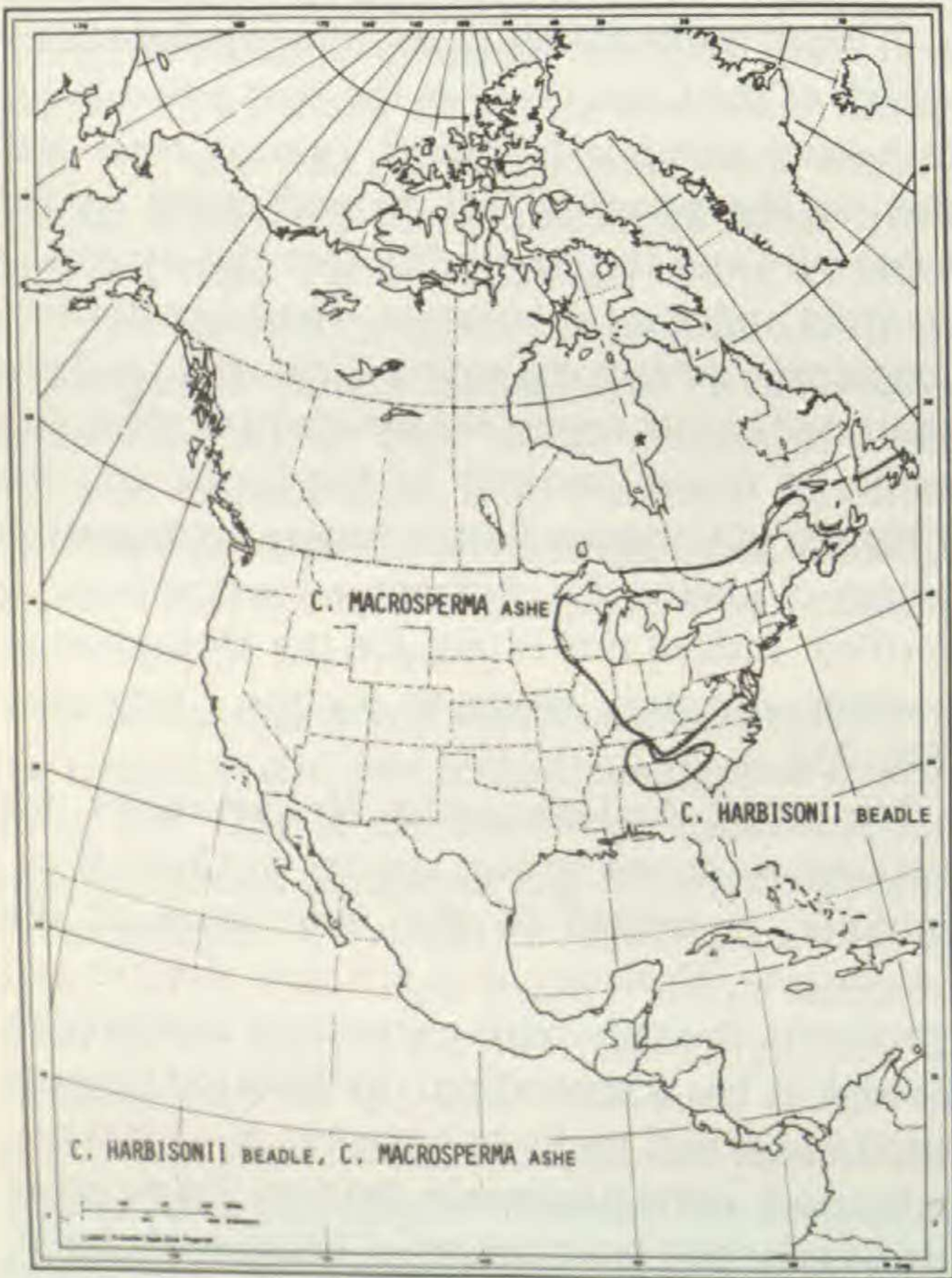


FIGURE 19. Distribution of *Crataegus*: *C. macrosperma* Ashe, *C. harbisonii* Beadle.



FIGURE 21. Map showing richness of species (no. per 640 km²) in North America.

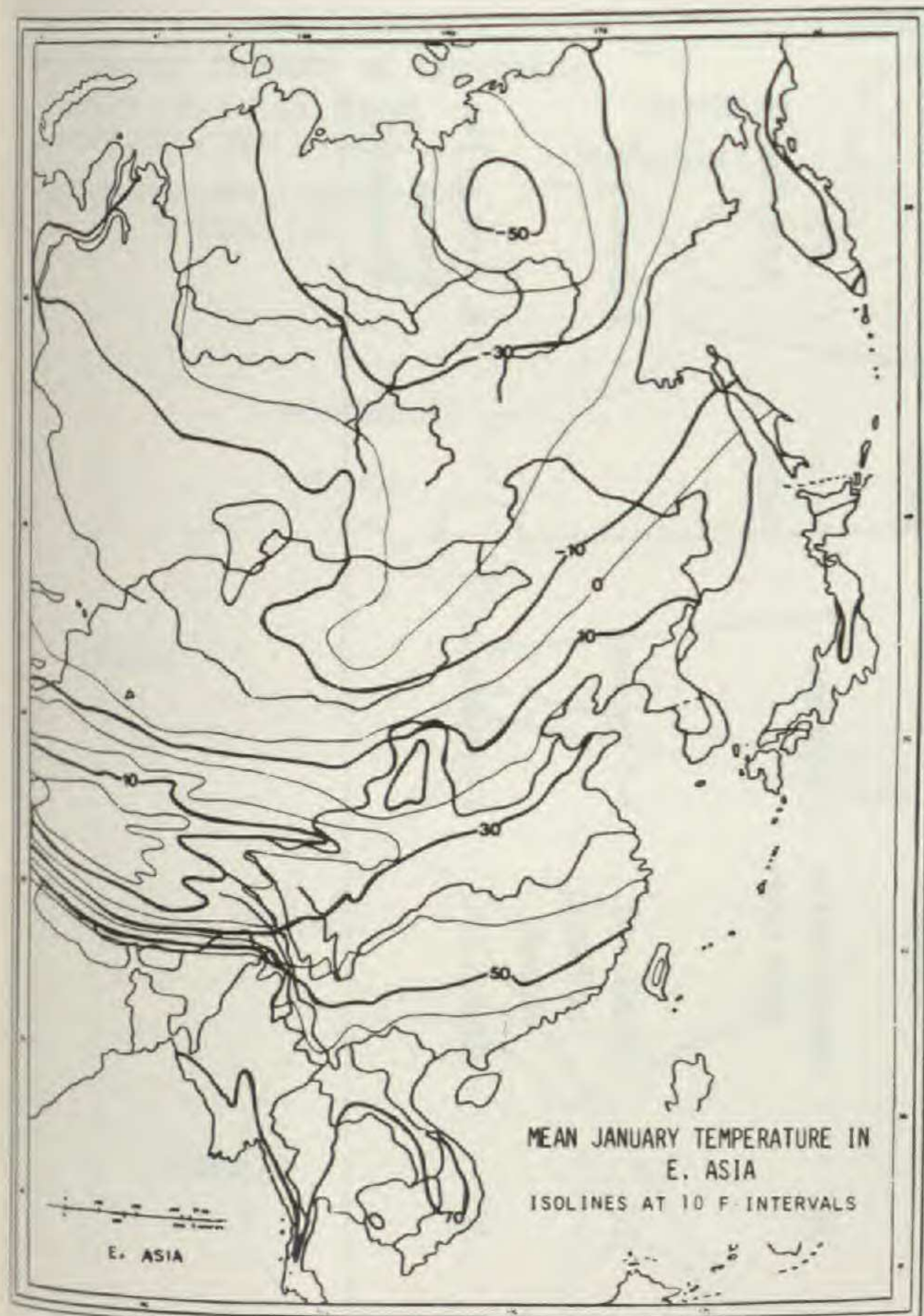


FIGURE 22a. January isotherms. Mean monthly data for eastern Asia. Note 10°F.

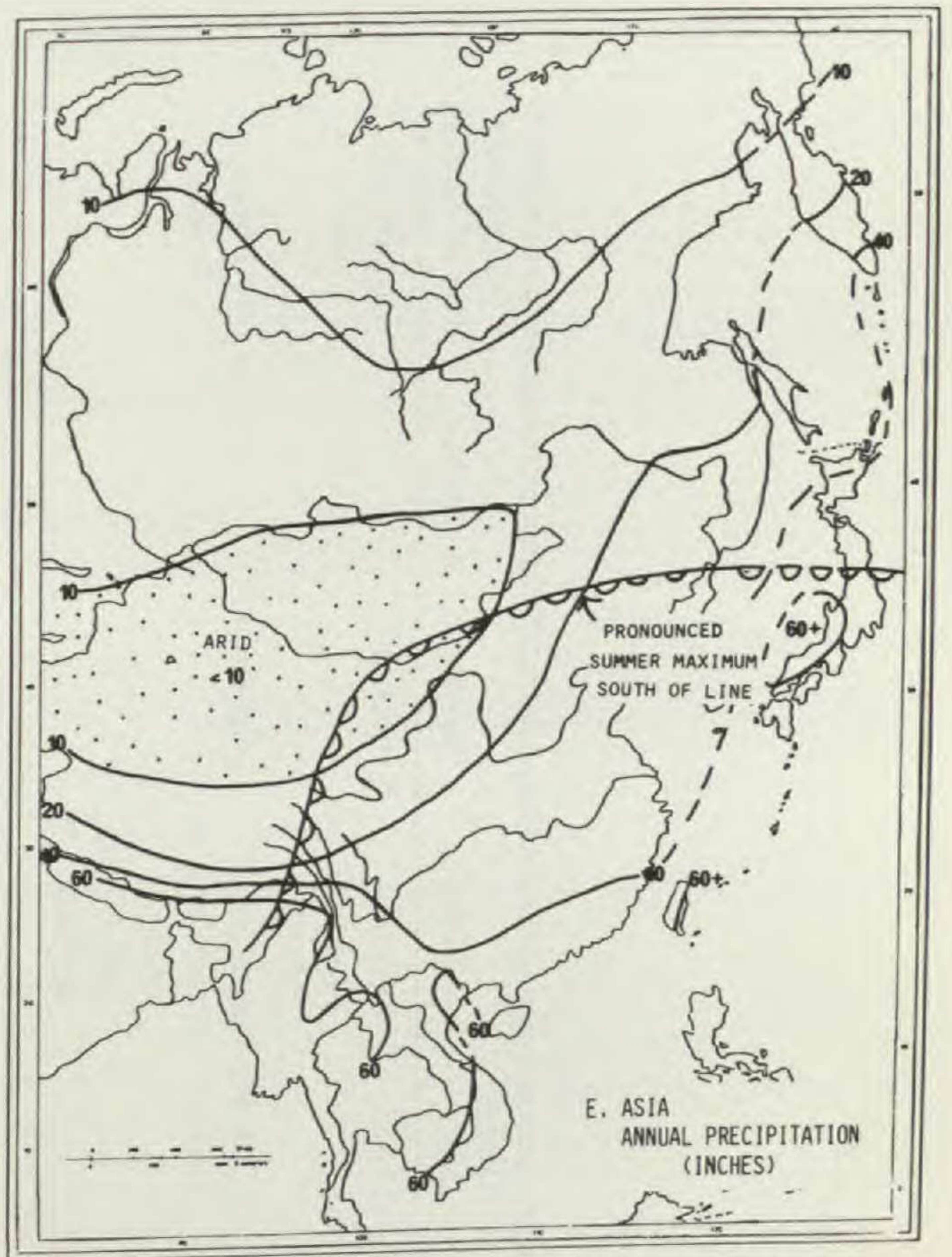


FIGURE 23a. Mean annual precipitation for eastern Asia. Note arid regions and summer maxima.



FIGURE 22b. January isotherms. Mean monthly data for North America. Note 10°F.

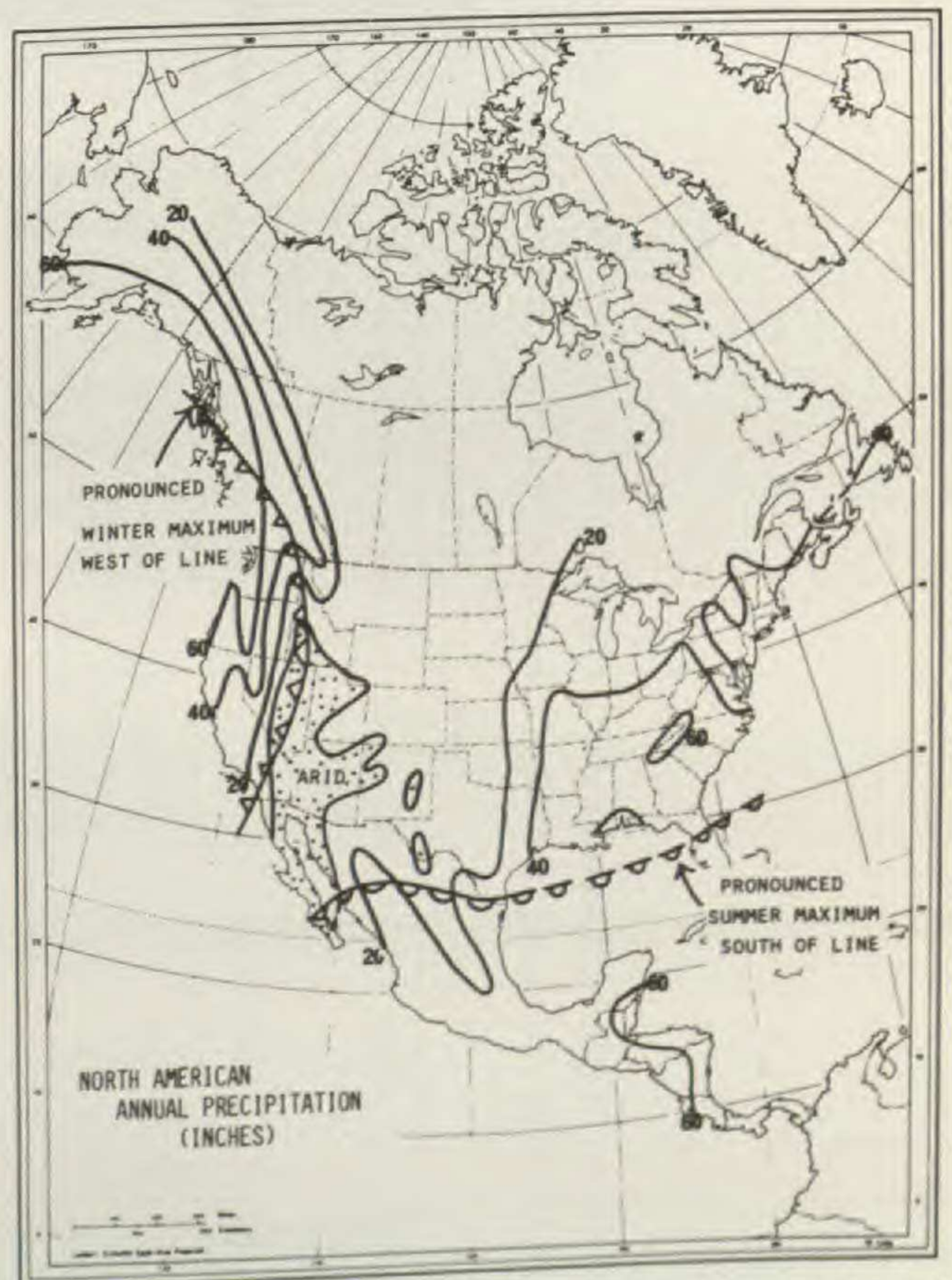


FIGURE 23b. Mean annual precipitation for North America. Note arid regions and winter maxima.

TABLE 8. Technical characteristics of the genera of the tribe *Crataegeae*.

	Habit	Thorns	Leaves	Inflor.	Flowers	Petals	Stamen No.	Pome	Seeds	Others	Distribution No. of Species
<i>Mespilus</i>	small tree	thorny short shoots	simple, large	single, on leafy shoots	large, white	round	30–40	medium; open; brown	5 pyrenes		Europe, W. Asia 1
<i>Crataegus</i>	small shrub to small tree	thorny short shoots or short shoots & thorns	small, unlobed to deeply lobed	corymb	small, white	± round	5, 10, 15, 20	small to medium; sl. open; yellow, red or black	1–5 pyrenes		N. Temp. ≈ 140
<i>Pyracantha</i>	shrub	thorny short shoots	small, serrate; evergreen	corymb	small, white	± round narrow	20	small; red; closed	5 pyrenes	2 ovule/carpel	Eurasia 9
<i>Hesperomeles</i>	shrub or small tree	shoots, sometimes thorn-tipped	small coriaceous, evergreen	corymb	small, white or pink	round	20	small; red or dark berry	5 pyrenes	1 ovule/carpel	C. & S. America 10
<i>Cotoneaster</i>	small to large shrub	thornless	small, entire	cyme	small, white	± round	20	small; red or black; closed	2–5 pyrenes		Eurasia 100
<i>Osteomeles</i>	tree or shrub	slight tendency to short shoots	evergreen, pinnate	corymb	small, white	irreg. obovate	20	fleshy	5 pyrenes		E. Asia to Polynesia (Hawaii) 3.

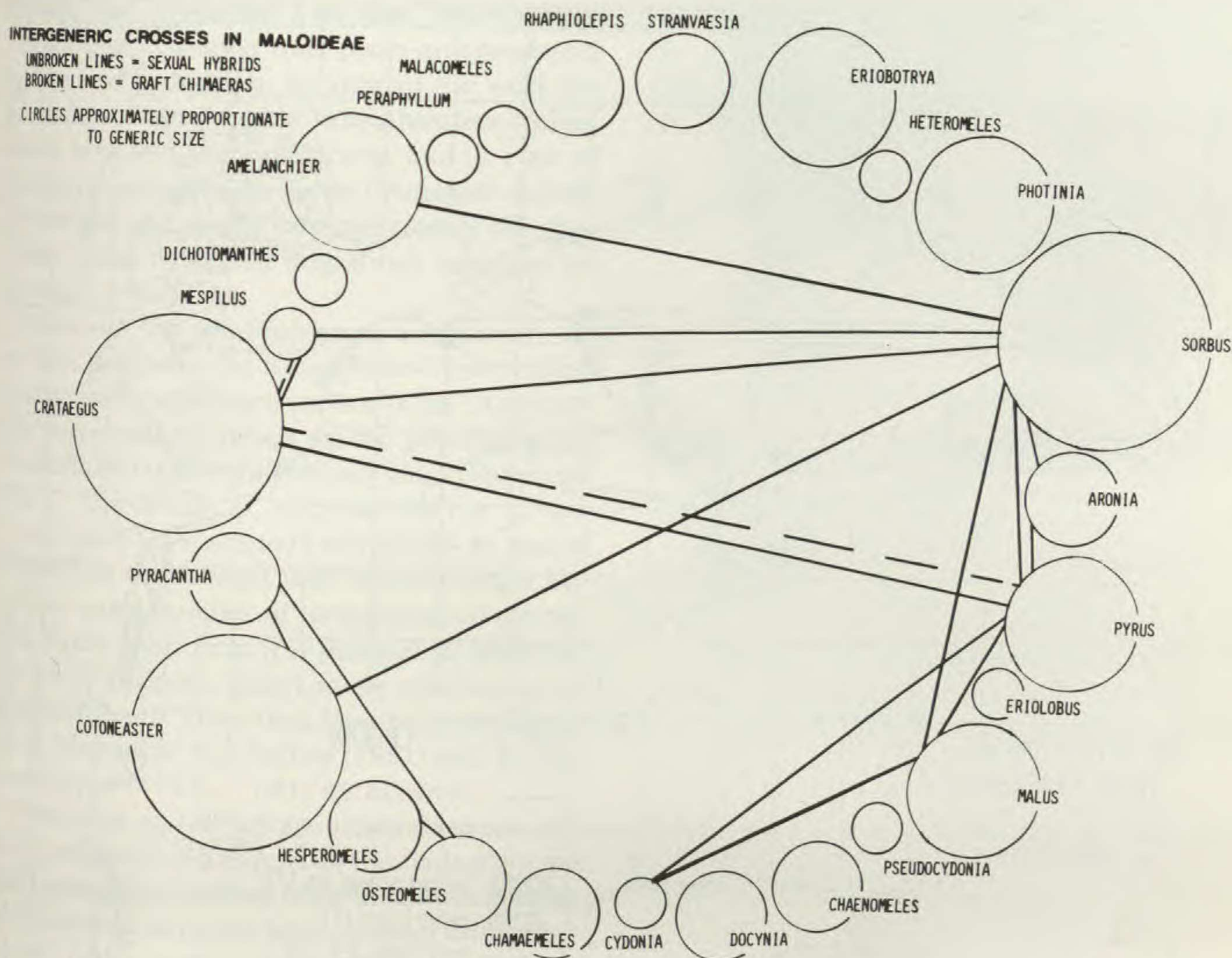


FIGURE 24. Intergeneric crosses recorded in Maloideae (after Robertson, 1974).

cident with a climatic deterioration. A variant of this suggested by D. Axelrod (pers. comm.) will derive *Hesperomeles* from *C. mexicana* or an extinct relative, with similar southward spread. A northward migration to Panama-Costa Rica could be very recent. *Pyracantha*, the other truly thorny *Crataegeae*, has about ten species. It is subevergreen and predominantly warm humid southeast Asian. It is most like *Crataegus*. The non-thorny *Cotoneaster* is a large and quite variable genus widespread in Eurasia, especially temperate Asia. It is not too different from *Pyracantha* but is distinct chemically (Challice, 1981). *Mespilus* is Taurian-Anatolian and is biogeographically, as well as morphologically, well removed from the core of the tribe. It is a candidate hybrid origin genus. The pinnate leaf, specialized habitat, and remarkable distribution of *Osteomeles*, with its Hawaiian disjunction and sea-shore habitat, permits one to discount it as ancestral.

Pyracantha thus represents the nearest sister group (see also Fig. 26, Table 8) and the biogeo-

graphic aspect of adaptive radiation in *Pyracantha-Crataegus-Hesperomeles* is most efficiently postulated from a southwest China base with primitive *Crataegus* emerging in that area, and now being represented only by *C. scabrifolia* (Fig. 27). Diversification to Western Eurasia has probably only occurred once or twice on the basis of present biogeography and the existence of major barriers in Central Asia, and in this one may consider the early Tertiary Turgai Straits. The Beringian route has been available geographically throughout the Tertiary but available climatically only intermittently (Wolfe, 1977), perhaps only in the Eocene, Middle Miocene, and in certain interglacials. The major groups of *Crataegus* are preponderantly different in North America from Eurasia, which together with the diversities in North America itself are clearly indicative of several independent movements Asia to North America via Beringia, followed by southward range collapse in both continental areas.

In general, correlated suites of characters found

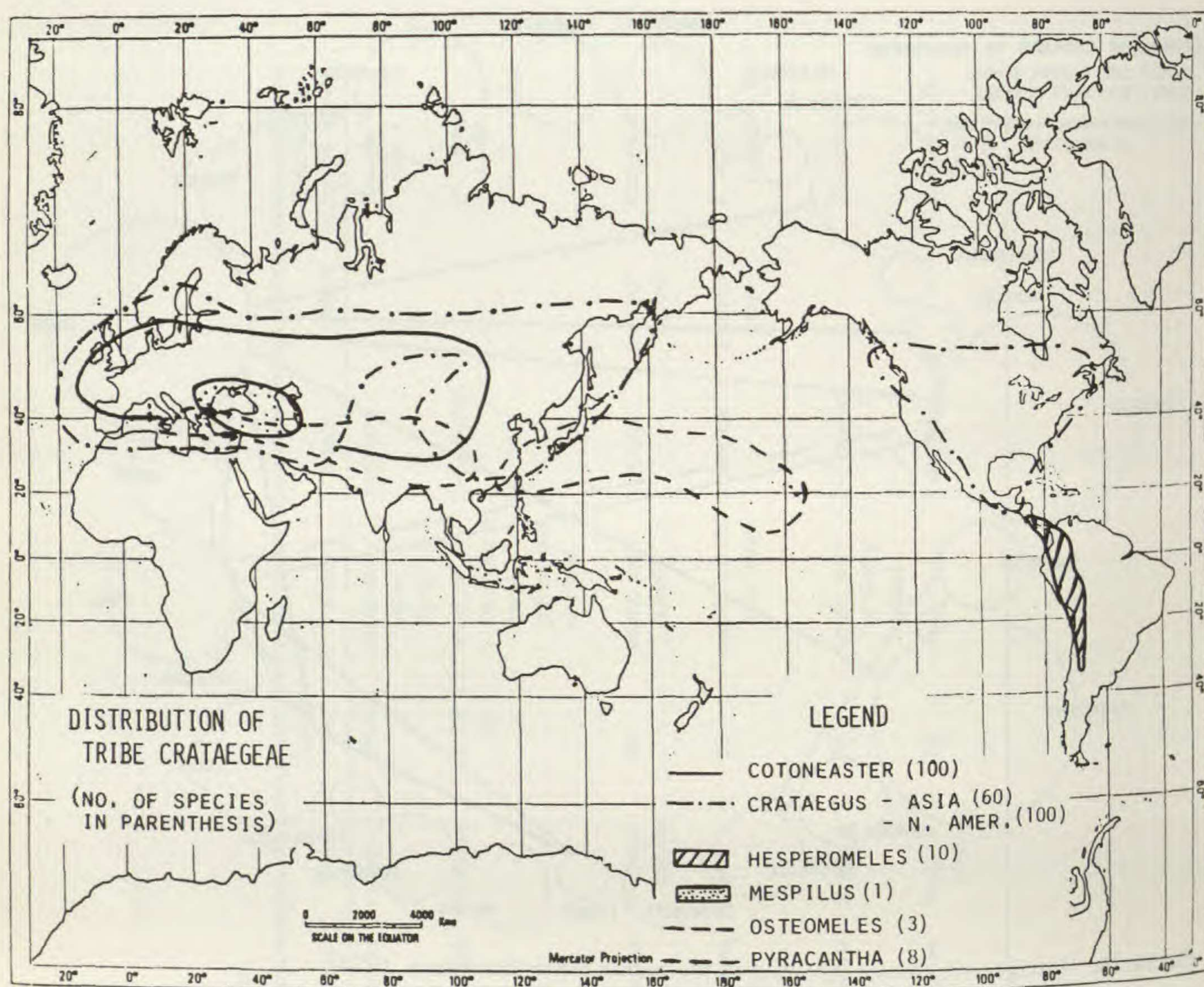


FIGURE 25. Distribution map of crataegean genera.

in the majority of crataegean genera are considered ancestral, and, in cladistic terminology, are symplesiomorphic. Apomorphic states are logically derived. Figures 29 to 31 summarize diagrammatically certain presumptive evolutionary trends in *Crataegus*, and Table 5 presents the total character set used.

CLADISTIC RESULTS

Figure 28 is a computed pro-cladogram for the 75 OTUs used in the taxonomic work. The target diagram format is used because the cladistic predicates permit apomorphy counts (= advancement indices) and because of spatial requirements (numerous OTUs) on the diagram. Computation was stopped, or the results not plotted, when patristic distance exceeded eight units and where several different fusions of similar parsimony in longer stems (± 2 units) were possible. Thus many of the major groups, viz. Chinese and Siberian alliances (including sect.

Sanguineae), and other American and south-eastern United States taxa are not tied into the central core of the genus. However, the critical centre, including *C. scabrifolia* and *C. mexicana*, is tied in. *Azaroli* and *Oxyacanthae*, however, seem relatively reliably connected to the core of the genus.

Therefore, with some exceptions, the cladogram proposed unites only the tightly-knit groups. In doing so, it strongly reflects the phenetic results and it also conforms with the biogeographic results. Nevertheless, to mindlessly push the cladogram through to completion at this stage, in my opinion, would be a fundamental mistake with the relatively few characters polarized. Had it been possible to polarize more characters, some of the ambiguities may well have been resolved. For instance, it is critical to discover whether the 'Americanae' are best derived from the *Sanguineae*, which would optimize (i.e. generate greater cladistic parsimony), in general, on the development of thorns, of leaf-shape, climatic adap-

tations, etc., or whether a parallel '*Americanae*'-*Sanguineae* evolution took place independently on the two continents. In view of the weak relationship of '*Americanae*' to southeastern United States taxa and to *C. mexicana*, and in view of the fairly numerous Neogene *Crataegus* records (of various leaf shape) from the west of the continent, extra Beringian migrations represent an attractive viewpoint.

However, the pro-cladogram as currently set up does not make the *Sanguineae*-'*Americanae*' connection very attractive; but if the '*Americanae*' were radially raised on the pro-cladogram (= additional synapomorphies) a link from species like *C. kansuensis*, *C. maximowiczii* or *C. aurantia* becomes extremely attractive. In lieu of attempting the difficult task of polarizing a significant extra number of morphological characters, in the short term it is planned to substitute the use of phenolic assays in the clarification of group structure. These data have been found useful in *Maloideae* by Challice (1981) and Sinnott and Phipps (1983).

Note that as fusions are made between currently unconnected groups on the cladogram this will increase the number of definite homoplasies. Homoplasies have not been counted but are evidently highly numerous, but this is conformable with our biological understandings of *Crataegus* reproductive behaviour.

Another reason for caution in accepting long computed patristic distances lies in the polyploid and hybrid nature of *Maloideae*. The tribe is of postulated allopolyploid origin (maloid $x = 17$ from $x = 8 + x = 9$), numerous intergeneric hybrids are known (some in nature) and some involving *Crataegus* (notably with *Mespilus*) while proven and plausibly suspected hybridization in *Crataegus* is frequent (Phipps, 1984). Thus, long patristic unions as computed in standard programs might totally override and obscure actual hybridization events. This reinforces the rationale for leaving the published situation at the developmental stage of the pro-cladogram in 1982 until new data are analyzed.

DISPERSAL ABILITY

Pomes of *Crataegus*, as well as those of other similar berry-like fruit about 1 cm size, are commonly considered to be bird-dispersed (Phipps & Muniyamma, 1980). If this is so, then the potential for long-distance dispersal (LDD) immediately becomes a prominent consideration.

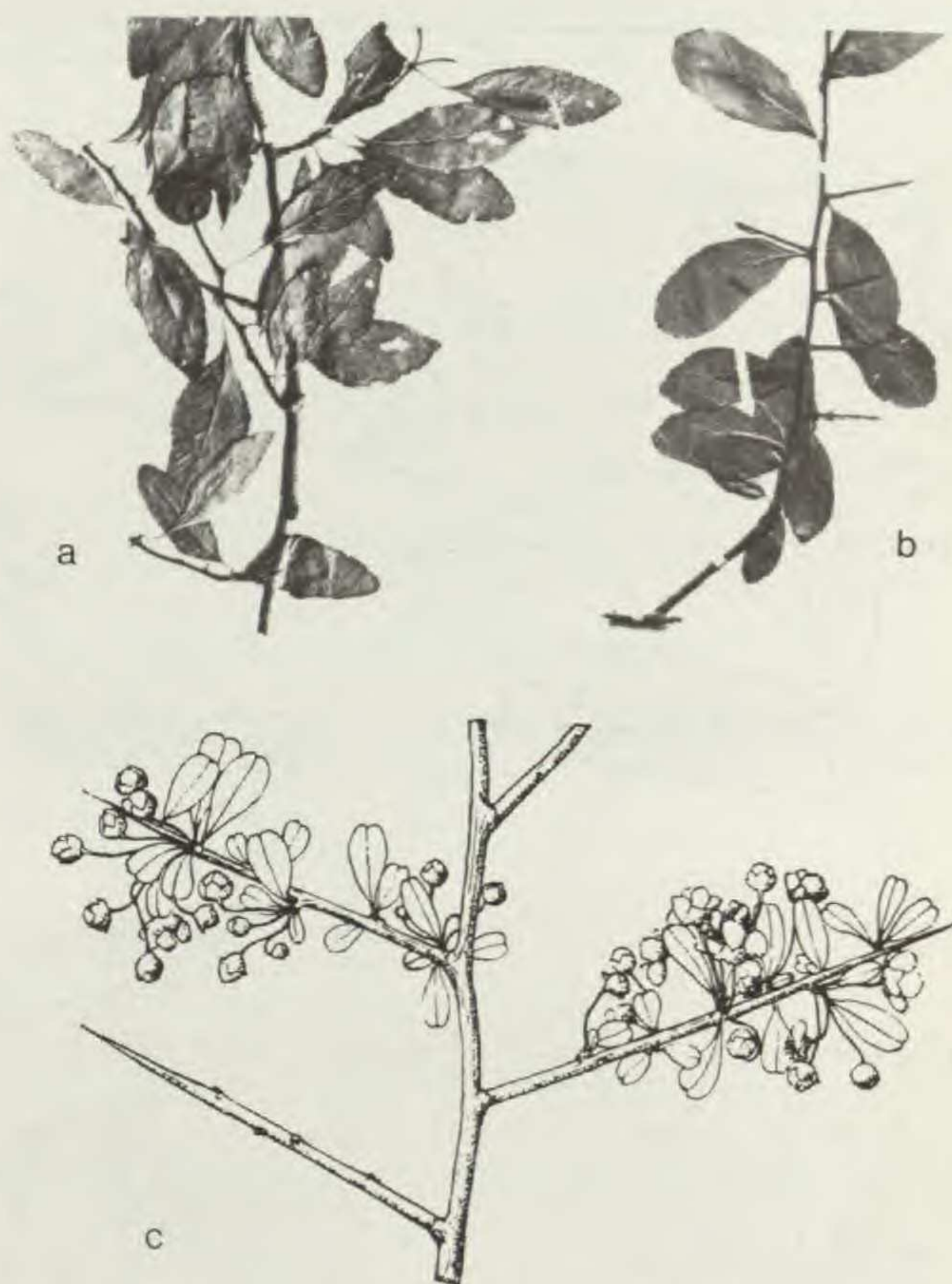


FIGURE 26. *Pyracantha crenulata* (lower), *Crataegus mexicana* (top left) and *C. scabrifolia* (top right) compared. Note leaf-shape and spiny short-shoots.

What is remarkable, however, is the paucity of hard data on *Crataegus* dispersal (e.g. DeBoer, 1979). Information, such as it is, is related to what eats *Crataegus* berries, and not how far seeds may travel in the gut of the fructivore. There is no question that several species of passerines and game birds eat *Crataegus* fruit. They may also do so in the autumn, while on migration. Birds during migration may lose course, due to navigation problems or by being storm driven. Numerous records attest to such birds ending up on the 'wrong' side of the Atlantic or Pacific Oceans. However, were such LDD to be a significant cause of *Crataegus* distribution patterns then it is inferred that taxonomically like kinds of *Crataegus* would be more commonly found than is actually the case on opposing sides of the major northern oceans. Indeed, the explanation of the distribution of only southeastern United States *C. marshallii* (related to ser. *Oxycanthae* of Europe), and possessing the smallest size of *Crataegus* fruit (3×6 mm), is aided by LDD concepts for a parsimonious explanation of its location. The extreme differences between the North American and European *Crataegus* floras indicate the effective closure of Atlantic route to

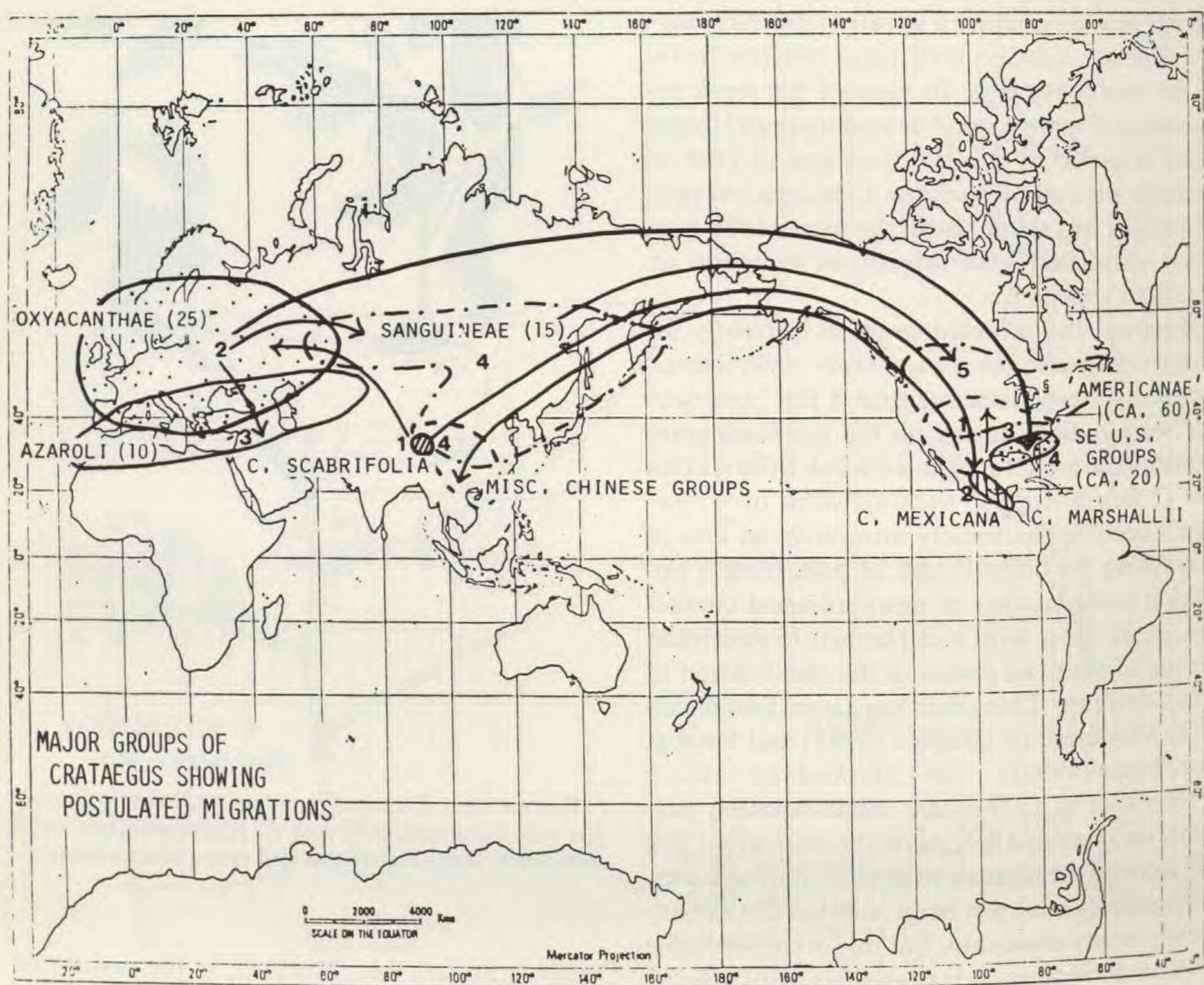


FIGURE 27. Major groups of *Crataegus* showing postulated migrations. Non-bracketed numbers trace the sequence.

Crataegus during most or all of *Crataegus* evolution. In view of the Atlantic situation, the East Asian-American taxonomic differences, and with the avian potentials being essentially equivalent, LDD across the Pacific must also be stochastically discounted. Both ungulates and rodents eat *Crataegus* fruit and seeds but they can hardly be agents of LDD.

Thus, short-distance dispersal (SDD), the effects of which are abundantly observed in nature, for instance in the rapid establishment of new *Crataegus* populations, is certainly adequate to explain dispersal and radiation between the two northern continents. Short-distance dispersal through Beringia thus remains the only serious candidate migration route and it is proposed as occurring whenever the Beringian climate permitted *Crataegus* to migrate to and thrive in the Chukchi-Alaska region.

PALEONTOLOGICAL CONSIDERATIONS

The Alaskan-Asian contact in Beringia has remained essentially unchanged geographically,

from the standpoint of this paper, since the early Tertiary. Rotation of plates on an Alaskan fulcrum, terrane accretion, etc., are of great interest to geologists but of less significance to this study. The sea gap, however, is of more consequence, and its exact extent in Beringia through the Tertiary is apparently not easy to establish. The consensus, however, is that it was usually narrow and with or without intervening small islands it has probably been a negligible SDD barrier throughout. Sea-level fluctuation through the Pleistocene must certainly have varied the width of this barrier and could have been one of the factors that affected timing of any Pleistocene *Crataegus* SDD. Clearly, however, the critical factor for the Beringian route is paleoclimate.

It is, therefore, posited that during climatic optima there is no significant barrier to American or east Asian *Crataegus* approaching Beringia using SDD. The Tertiary and Quaternary paleoclimate of Beringia are, therefore, of some interest. Firstly, Beringia has been at high latitudes throughout the Tertiary. Indeed, during the

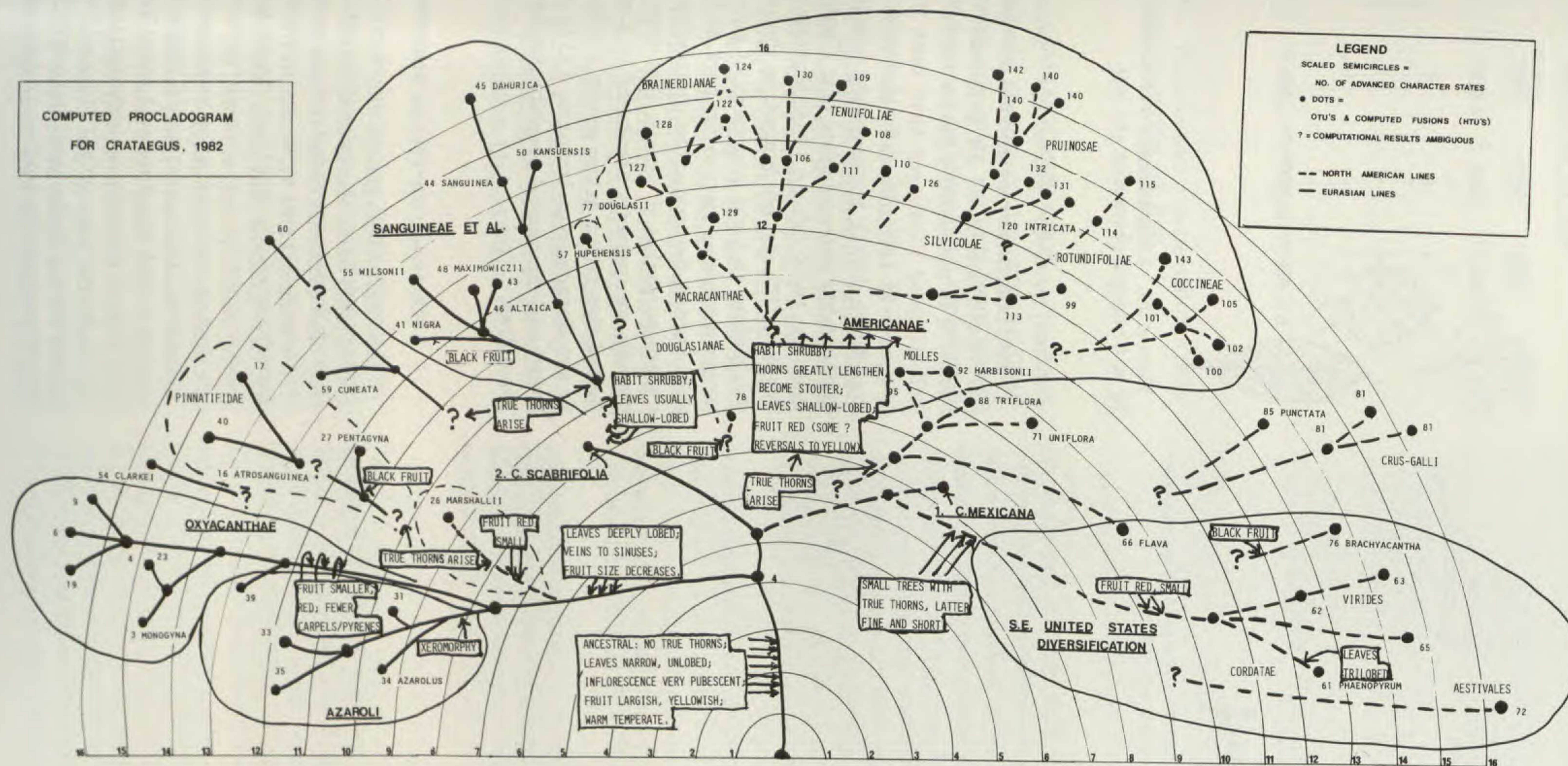


FIGURE 28. Pro-cladogram of 75 species of *Crataegus* based on 18 characters. (OTU numbers cross-referenced to Appendix A.)

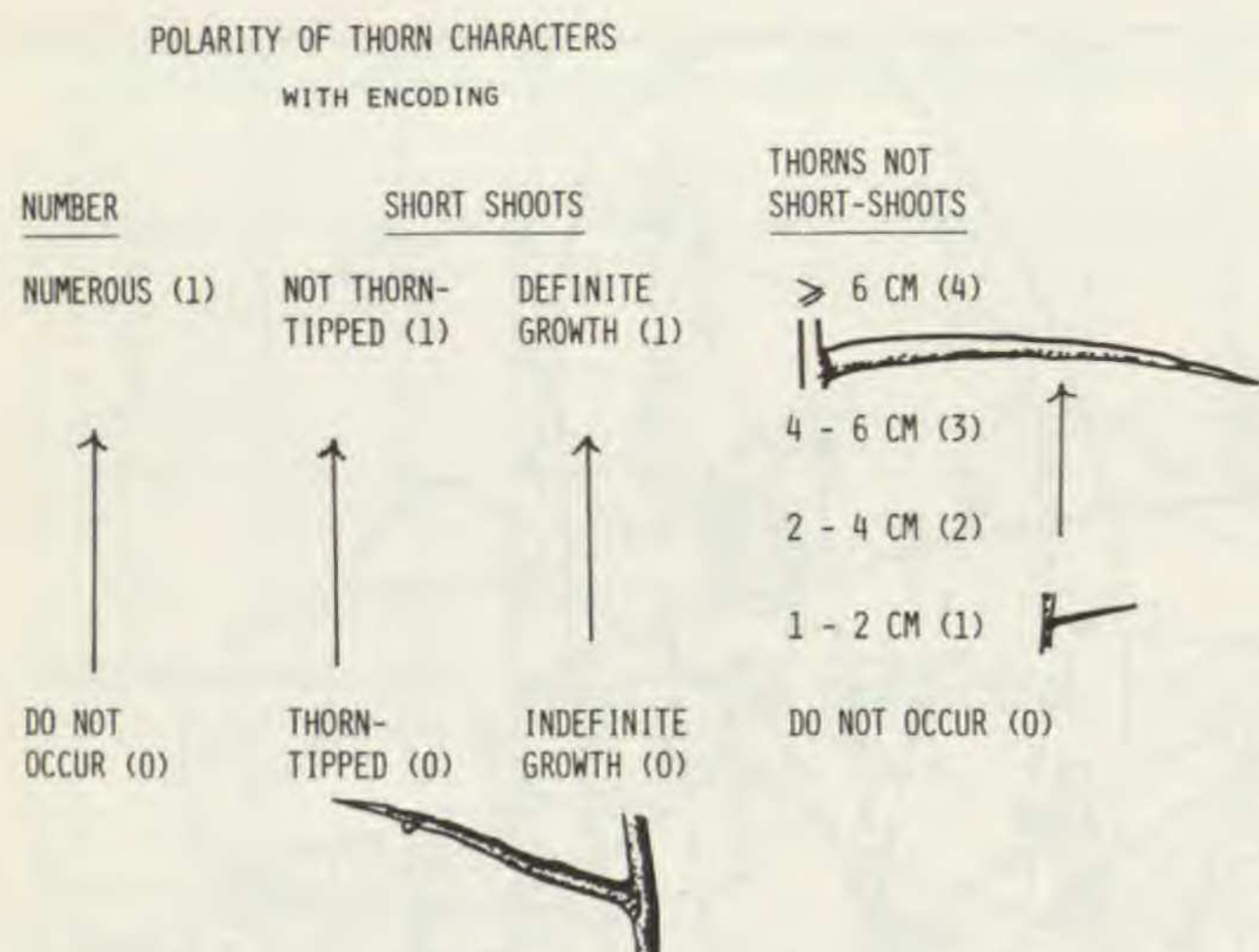


FIGURE 29. Diagrammatic representation of polarity in *Crataegus* characters: (a): thorn.

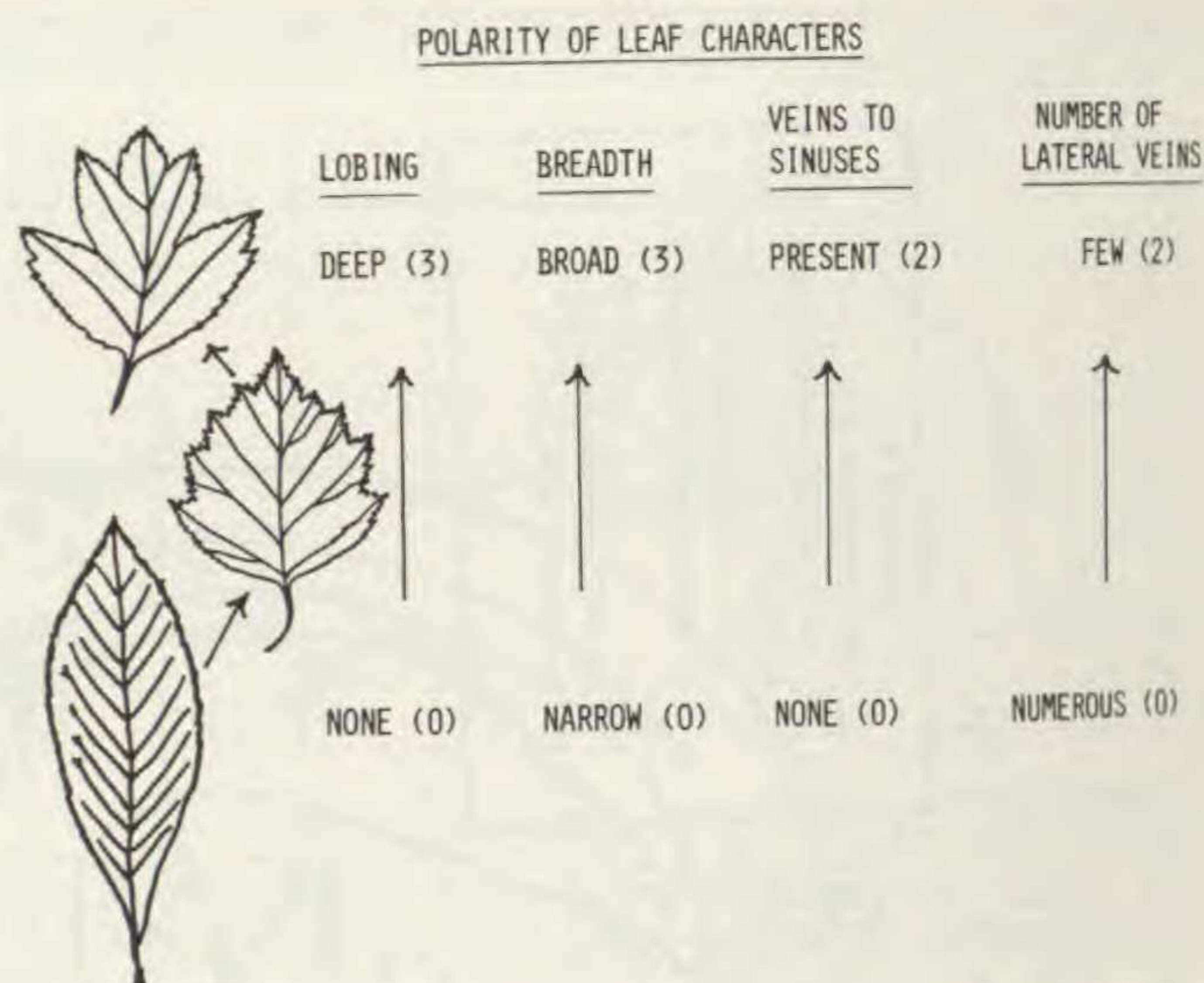


FIGURE 30. Diagrammatic representation of polarity in *Crataegus* characters: (b): leaf.

Eocene, the North Pole was in the (present) Chukchi Sea. Data on northern Hemisphere climate changes, however, indicate optima in the Eocene, middle Miocene, and possibly, certain interglacials (e.g. Lamb, 1977). The northern limits of extant *Crataegus* are, however, well to the south of Beringia, and these seem to be cold-hardy, phyletically advanced species (e.g. *C. sanguinea*, *C. aurantia*, *C. maximowiczii*, *C. chlorosarca*, *C. altaica* (Asia), and *C. douglasii*, *C. chrysocarpa* (N. America)).

It is inferred, therefore, that *Crataegus* crossed (and perhaps re-crossed) Beringia a limited number of times, during climatic optima. The Alaskan warm-climate interludes are well discussed by Wolfe (1971, 1977). A possible scenario is:

a) *Eocene event*

Ancestral *Crataegus* to Beringia, followed by range collapse southward on both continents with the vicariants *C. mexicana* becoming an ancient relict now settled in Mexico and *C. scabrifolia* in Yunnan.

b) *Miocene event*

Ancestral sect. *Sanguineae* types, e.g. *C. maximowiczii* types to Beringia, likewise followed by range collapse southwards and extensive radiation of ancestral and descendant taxa on both sides of the Pacific.

Fossil benchmarks would help secure the dates in question, as would a more detailed knowledge of Beringian paleoclimate. Nevertheless, it would seem that substantial time intervals are required to permit the degree of evolution observed. A telescoping of the proposed time-scale is possible as long as event (a) is not much later than Miocene on general evolutionary considerations.

FOSSIL BENCHMARKS

Fossil benchmarking appears to require a critical re-evaluation of all proposed *Crataegus* fossils. It is noteworthy that some for-a-period well-accepted *Crataegus* have been transferred to genera as taxonomically unrelated as *Alnus* (e.g. Wolfe, 1971). However the collected works of reputable palentologists (e.g. Chaney, 1927; Lamotte, 1936; Oliver, 1936; MacGinitie, 1934; Wolfe, 1977) etc. are bound, in the opinion of this author, to yield a number of genuine *Crataegus* records at least as far back as the Oligocene. Indeed, the unique leaf morphology of some *Crataegus* makes it certain that some existing records are correctly attributed to *Crataegus* if indeed, they match extant genera. Projection back to the Eocene (e.g. Lamotte, 1952) is far less secure and this period possibly saw the origin of Maloideae.

DISPERSAL OF OTHER MALOIDS

Of the maloidean genera only five (*Crataegus*, *Sorbus* [only subg. *Aucuparia*], *Malus*, *Amelanchier*, and *Photinia*) occur in both northern macrocontinents (Table 9). While the fruits of *Chaenomeles*, *Cydonia*, and some others are large, in general maloid pomes are small (about the same as *Crataegus* in variability). Their patterned distribution likewise must surely indicate either very modern evolutionary diversification in the whole tribe or poor LDD. Obviously the latter hypothesis conforms best to the *Crataegus* argument. Indeed for the entire Maloideae, LDD explanations are cogent for only three species—*Cratae-*

POLARITY OF SOME FRUIT CHARACTERS

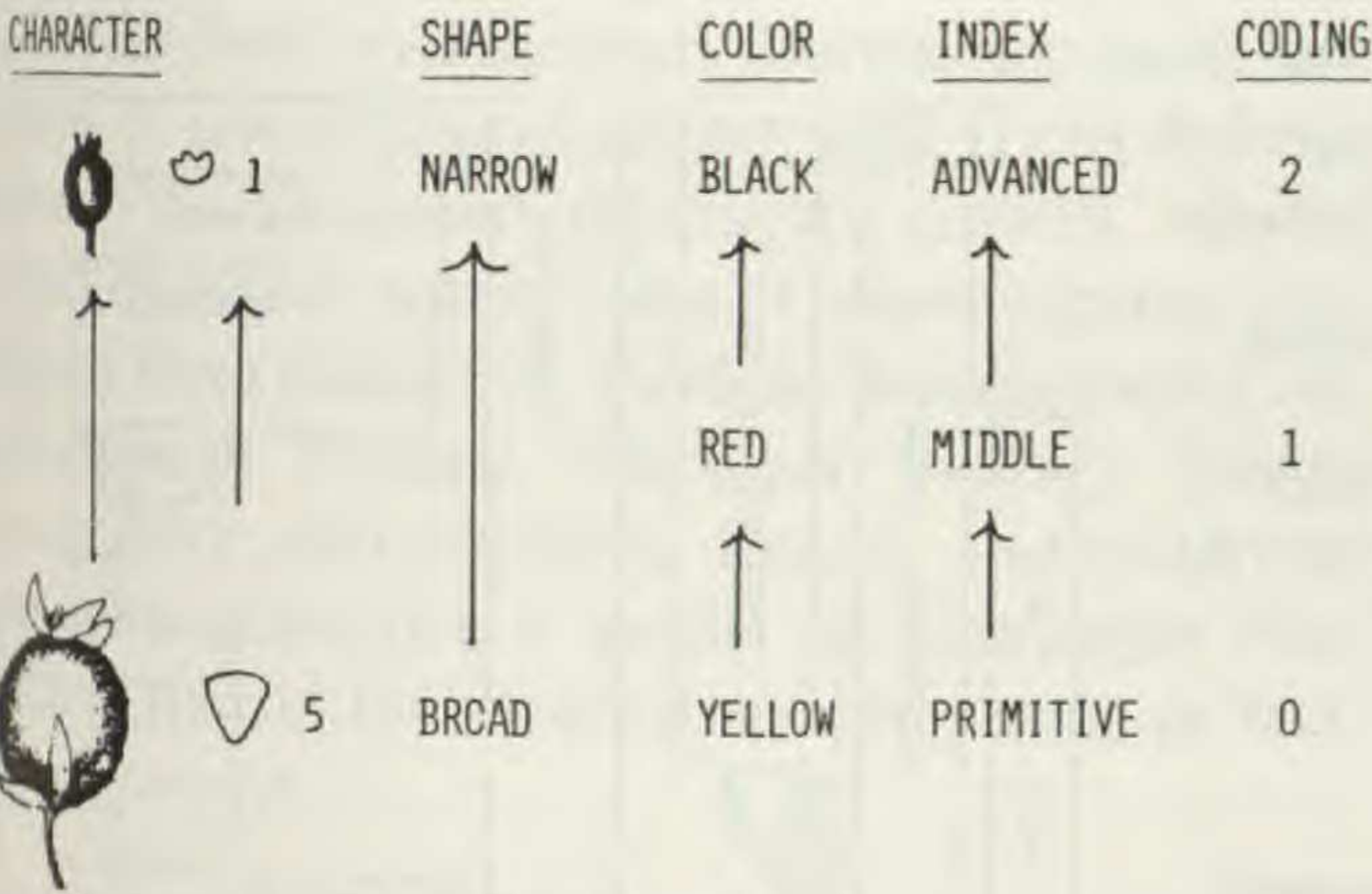


FIGURE 31. Diagrammatic representation of polarity in *Crataegus* characters: (c): fruit.

gus marshallii, *Chamaemeles coriacea* (endemic to Madeira), and *Osteomeles anthyllidifolia* (Hawaii) although this latter, disjunct from eastern Asia, could have an anthropogenic explanation.

TAXONOMY OF UNITED STATES *CRATAEGUS*

The wide variety of apparently not closely-related forms restricted to the southern United States (e.g. *Microcarpae*, *Aestivales*, *Virides*, *Flavae*, *Brevispinae*) is indicative of a relictual flora that had diversified long in the past. The above groups offer little parallel to Asiatic forms except for hypothetical symplesiomorphies between *Virides* and *C. hupehensis*. The weak relationships between southern United States groups and other North American forms, e.g. ‘*Americanae*,’ *C. crus-galli*, and *C. mexicana* has already been noted. It is fascinating to be able to postulate a group of southeastern United States relicts.

TAXONOMY OF CHINESE *CRATAEGUS*

Most Chinese species are fairly closely inter-related, in two subgroups, the northern *Sanguineae* alliance and the slightly more southern *kan-suensis* alliance. It is these two sub-groups that relate most closely to North American *Crataegus* in the group ‘*Americanae*.’ *Crataegus cuneata* of southeastern China, however, is very distinct from other Chinese taxa, as is *C. hupehensis*, this plant having a remarkable leaf-shape and appearing to be thornless, whereas *C. scabrifolia* is quite unlike other Chinese species as already discussed. These last two probably represent old phylads, *hupehensis* perhaps representing the only

TABLE 9. Listing of maloid genera geographically (showing numbers of species per genus).

	Euras.	Am.
<i>Tribe Crataegeae</i>		
<i>Mespilus</i> (1)	1	—
<i>Crataegus</i> (150)	55	95
<i>Pyracantha</i> (8)	8	—
<i>Hesperomeles</i> (9)	—	9
<i>Osteomeles</i> (3)	3	—
<i>Cotoneaster</i> (100)	100	—
? <i>Dichotomanthus</i>	1	—
<i>Tribe Sorbeae</i>		
<i>Docynia</i> (5)	5	—
<i>Chaenomeles</i>		
incl. <i>Pseudocydonia</i>	5	—
<i>Cydonia</i> (1)	1	—
<i>Malus</i> (45)	40	5
× <i>Malosorbus</i> (1)	1	—
<i>Eriolobus</i> (1)	1	—
<i>Pyrus</i> (45)	45	—
<i>Eriobotrya</i> (30)	30	—
<i>Photinia</i> (50)	45	5
<i>Heteromeles</i> (1)	—	1
<i>Stranvaesia</i> (6)	6	—
<i>Rhaphiolepis</i> (8)	8	—
<i>Sorbus</i> (125)	120	5
<i>Aronia</i> (3)	—	3
<i>Chamaemeles</i> (1)	1	—
<i>Amelanchier</i> (18)	6	12
<i>Malacomeles</i> (2)	—	2
<i>Peraphyllum</i> (1)	—	1

east-west Beringian *Crataegus* migration. *Crataegus tangchungchangii* is inadequately known.

SUMMARY

Phenetic and biogeographical analysis shows a very strong patterning of *Crataegus* species-groups in regions. Among these, *Azaroli* and *Oxyacanthae* of Europe and Western Asia are particularly distinct. The Siberian sect. *Sanguineae* and allies have much in common with North American ‘*Americanae*’ in spite of usually separating slightly when subjected to numerical taxonomic analysis. In the United States and Canada a varied group of southern species distinguish rather well from the more northern ‘*Americanae*’ species. Apparent vicariants *C. scabrifolia* and *C. mexicana*, without true thorns, occur in Yunnan and Mexico respectively.

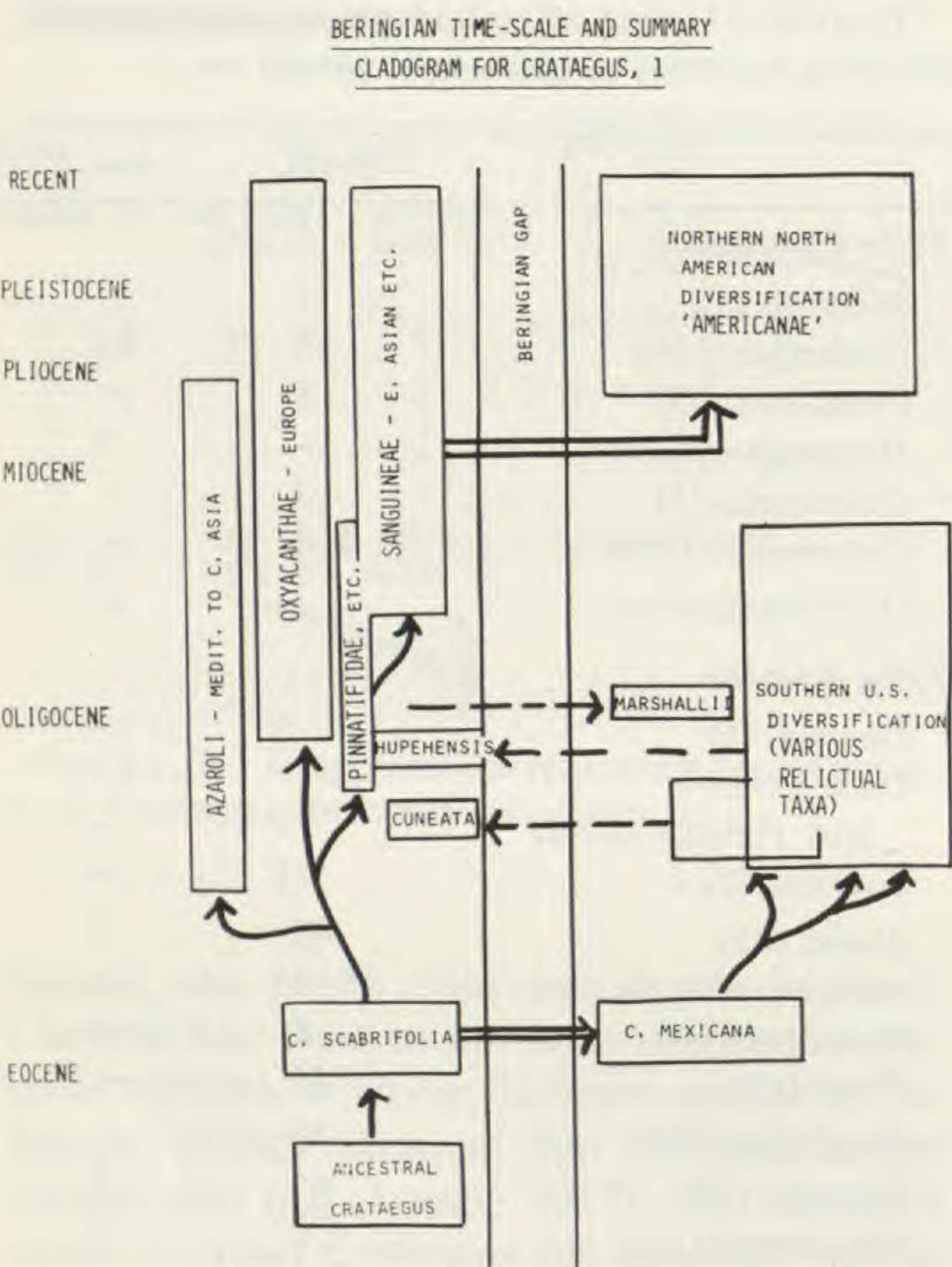


FIGURE 32. Simplified vicariance cladogram illustrating preferred theory (see text for fuller explanation).

Cladistic analysis is based on generating pleiomorphies from the natural tribe Crataegeae and indicates remarkable similarities between *Pyracantha*, *C. scabrifolia*, and *C. mexicana*. The cladistic algorithm was not pursued to completion due to ambiguities about how major groups might be connected. These ambiguities are reinforced by knowledge of potential for wide hybridization among Maloideae and also, specifically, within *Crataegus*.

Biogeographical thinking is thus brought into the cladistic argument, the reasoning resting strongly on the very low likelihood of LDD. The few plausible LDD events are noted. This makes the Beringian route the only significant contender during the Tertiary and requires climatic optima for SDD to move *Crataegus* through Beringia. But the frequency of this is considered relatively low on paleoclimatic grounds and the small number of similar *Crataegus* phylads on both sides of the Pacific. Fossil evidence, although requiring modern updating, suggests plentiful *Crataegus* in North America from the Mid-Tertiary. The origin of the genus is hard to time at present but

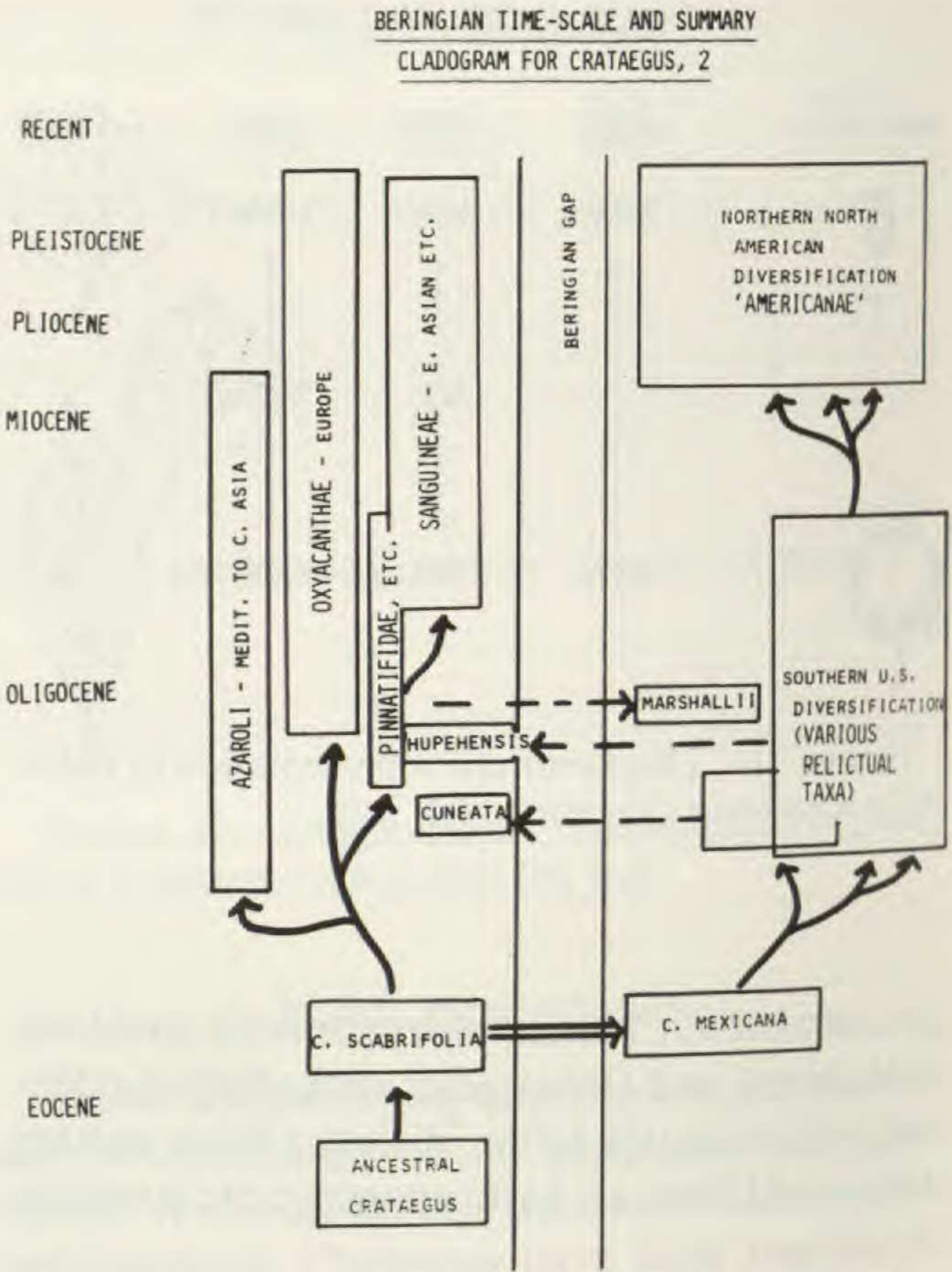


FIGURE 33. Simplified vicariance cladogram illustrating alternative hypothesis (see text for fuller explanation).

late Eocene can stand as the midpoint of several possibilities.

One is thus left with two broad evolutionary options, specifically, '*Americanae*' being derived from '*Sanguineae*' (Fig. 32), the most likely solution, in spite of certain difficulties with it, or parallel development in both macro-continent from *scabrifolioid* and *mexicanoid* stock after only one successful Beringian event (Fig. 33). The procladogram currently favors this, but only on gradistic grounds. This may well be changed by further evidence (and is challenged by known Alaskan migration potential). Not enough is known about some peculiar species, which may be intermediates between existing taxa, or relicts of older radiation. But not one of these bears on the choice between the two models presented above. A collapsing of the time-scale, which may prove necessary, as evidence accumulates, should not of itself affect the form of the cladogram.

Thus, *Crataegus* has changed, due to modern researches, from a genus in which taxonomy and cladistics had appeared overwhelmingly difficult, to, in some senses, the very opposite—a para-

digm of an SDD genus with long life history, evolving mainly during the Tertiary, and evidencing both evolutionary bursts, probable periods of phenetic gradualism, and, if our feelings about the proposed relicts are correct, almost total stasis in some cases. Overwhelming evidence from phenetics, modern biogeography, reproductive biology, dispersal biology, paleogeography, paleoclimate, fossils, and outgroup analysis, generates a model of *Crataegus* evolution that is the clearest to date, and, in fact, totally novel.

LITERATURE CITED

- BROWICZ, K. 1972. In P. H. Davis (editor), *Flora of Turkey* 4: 133–147.
- BYATT, J. I. 1975. Hybridisation between *Crataegus monogyna* Jacq. and *C. laevigata* (Poir.) DC. in south-eastern England. *Watsonia* 10: 253–264.
- . 1976a. The structure of some *Crataegus* populations in north-eastern France and south-eastern Belgium. *Watsonia* 11: 105–115.
- . 1976b. Pollen morphology of some European species of *Crataegus* L. and of *Mespilus germanica* L. (Rosaceae). *Pollen & Spores* 18: 335–349.
- , I. K. FERGUSON & B. G. MURRAY. 1977. Intergeneric hybrids between *Crataegus* L. and *Mespilus* L. a fresh look at an old problem. *Bot. J. Linn. Soc.* 74: 329–343.
- CHALLICE, J. 1981. Chemotaxonomic studies in the family Rosaceae and the evolutionary origins of the subfamily Maloideae. *Preslia* 53: 289–304.
- CHANEY, R. W. 1927. Contributions to paleontology. IV. Geology and paleontology of the Crooked River Basin with special reference to the Bridge Creek flora. Carnegie Inst.
- CINOVSKIS, R. 1971. Boyaritschniki Pribaltici. *Crataegi Baltici*. Riga. (In Russian.)
- DE BOER, J. I. 1979. Dispersal of *Crataegus* L. (hawthorn) in southwestern Ontario. UWO Plant Sciences Dept. Honours Project (unpubl.).
- DICKINSON, T. A. & J. B. PHIPPS. 1984. Taxonomic studies in *Crataegus* L. (Rosaceae: Maloideae). XIV. Short short leaf heteroblasty in *Crataegus crusgalli* L., sens. lat. *Canad. J. Bot.* 64. (in press.)
- & ———. submitted. Taxonomic studies in *Crataegus* L. (Rosaceae: Maloideae). XIII. Pattern of phenotypic variation in *Crataegus* section *Crus-galli* in Ontario. *Syst. Bot.*
- & ———. submitted. Taxonomic studies in *Crataegus* L. (Rosaceae: Maloideae). XV. The breeding system of *Crataegus crus-galli* L. sens. lat. in Ontario. *Amer. J. Bot.*
- EL-GAZAAR, A. 1980. The taxonomic significance of leaf morphology in *Crataegus* (Rosaceae). *Bot. Jahrb. Syst.* 101: 457–469.
- & A. A. BODAWI. 1977. Taxonomic significance of chromosome numbers and geography in *Crataegus* L. *Phytologia* 35: 271–275.
- FRANCO, J. A. 1968. *Crataegus*. In T. G. Tutin et al. (editors), *Flora Europaea* 2: 73–77.
- GLADKOVA, V. N. 1968. Karyological studies on the genera *Crataegus* L. and *Cotoneaster* Medik. (Maloideae) in relation to their taxonomy. *Bot. Žurn. (Moscow & Leningrad)* 52: 354–356.
- KRUSCHKE, E. M. 1965. Contributions to the taxonomy of *Crataegus*. Milwaukee Public Mus. Publ. Bot. 3.
- LAMB, H. H. 1977. *Climate, Past, Present and Failure*. McEwen, London.
- LAMOTTE, R. S. 1936. Contributions to paleobotany. V. The upper Cedarville flora of northwestern Nevada and adjacent California. Carnegie Inst.
- . 1952. Catalogue of the Cenozoic plants of North America through 1950. *Geol. Soc. Amer. Mem.* 51.
- LONGLEY, A. E. 1924. Cytological studies in the genus *Crataegus*. *Amer. J. Bot.* 11: 297–315.
- LOUDON, J. C. 1838. *Arboretum et Fruticetum Britannicum*. London.
- LOVE, R. & M. FEIGEN. 1979. Intraspecific hybridisation between native and naturalised *Crataegus* (Rosaceae) in western Oregon. *Madroño* 25: 211–217.
- MACGINITIE, H. D. 1934. Contributions to paleobotany. II. The Trout Creek Flora of southeastern Oregon. Carnegie Inst.
- . 1952. The Kilgore Flora. A Late Miocene Flora from Northern Nebraska. U.C.L.A. Public. *Geol. Sci.* 35: 67–158.
- MCGEARY, S. E. & A. BEN-AVRAHAM. 1981. Allochthonous terranes in Alaska: implications for the structure and evolution of the Bering Sea shelf. *Geology* 9: 608–614.
- MAIRE, R. 1980. *Crataegus*. In *Flore d'Afrique du Nord* 15: 130–142. Publ. Lechevalier, Paris.
- MUNIYAMMA, M. & J. B. PHIPPS. 1979a. Pollen meiosis and polyploidy in *Crataegus*. *Canad. J. Genet. Cytol.* 21: 231–241.
- & ———. 1979b. Cytological proof of apomixis in *Crataegus*. *Amer. J. Bot.* 66: 149–155.
- & ———. 1984. Studies in *Crataegus*. XI. Further cytological evidence for apomixis in North America hawthorns. *Canad. J. Bot.* 64. (in press.)
- OLIVER, E. 1936. Contributions to paleontology. I. A Miocene flora from the Blue Mountains, Oregon. Carnegie Inst.
- PALMER, E. J. 1953. *Crataegus*. In H. A. Gleason, New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada II: 338–375.
- PHIPPS, J. B. 1975a. Kilometric distance. *Canad. J. Bot.* 11: 1116–1119.
- . 1975b. Bestblock: optimizing grid size in biogeographic studies. *Canad. J. Bot.* 53: 1447–1452.
- . 1983. *Crataegus*—a nomenclator for section and serial names. *Taxon* 32: 598–604.
- . 1984. Problems of hybridity and cladistics in *Crataegus*. In W. F. Grant (editor), I.O.P.B. Conference, Montreal, Proceedings. Academic Press. (in press.)
- & M. MUNIYAMMA. 1980. A revision of *Crataegus* for Ontario. *Canad. J. Bot.* 58: 1621–1699.
- POJARKOVA, A. I. 1939. *Crataegus*. In V. L. Komarov, *Flora of the USSR* IX: 416–468. Botanical Inst. USSR, Leningrad.

- REHDER, E. 1940. *Manual of Cultivated Trees and Shrubs Hardy in North America*. 2nd edition. Macmillan, New York.
- RIEDL, K. 1969. *Crataegus*. In K. A. Rechinger (editor), *Flora Iranica* 66: 49–65.
- ROBERTSON, K. R. 1974. Genera of the Rosaceae in the southeastern United States. *J. Arnold Arbor.* 55: 621–654.
- RUSANOV, F. N. 1965. *Introdutsironavve boyaritschniki botanicheskogo sada an UzSSR*. In *Dendrologie Uzbekistanii*. (In Russian.)
- SARGENT, C. S. 1902. *Silva of North America*, Suppl. XIII: 31–184. Cambridge.
- . 1903. Recently recognized species of *Crataegus* in eastern Canada and New England, I. *Rhodora* 5: 52–60.
- SCHNEIDER, C. K. 1906. *Illustriertes Handbuch des Laubholzkunde* I: 766–802, 1001–1008. Fischer, Jena.
- SINNOTT, Q. P. & J. B. PHIPPS. 1983. Variation patterns in *Crataegus* § *Pruinosae* (Rosaceae) in southern Ontario. *Syst. Bot.* 8: 59–70.
- SMITH, P. G. & J. B. PHIPPS. 1980. Phenology of *Crataegus* flowering as a mechanism for reproductive isolation among related taxa. *Botany* 80. Vancouver. Abstract.
- STANDLEY, P. C. 1922. *Crataegus*. In *Trees and Shrubs of Mexico*, pt. 2: 335–336. United States National Museum.
- STERLING, C. 1964. Comparative morphology of the carpel in the Rosaceae. III. *Pomoideae: Crataegus, Hesperomeles, Mespilus, Osteomeles*. *Amer. J. Bot.* 51: 705–712.
- TIDESTROM, I. 1933. In H. E. Small, *Manual of the Southeastern Flora*, ed. 3: 637–644.
- WOLFE, J. A. 1971. Tertiary climatic fluctuations and methods of analysis of tertiary floras. *Paleogeogr. Paleoclimatol. Paleoecol.* 9: 27–57.
- . 1977. Paleogene Floras from the Gulf of Alaska Region. Washington, D.C.
- YÜ, T. & T. KU. 1974. *Crataegus*. In T. Yü, *Flora of the Peoples' Republic of China* 36: 186–206.

APPENDIX A. PROVISIONAL CHECKLIST OF WORLD *CRATAEGUS*

Arranged by section and series. ? = assignment to this section or series uncertain. Subscripted numbers, e.g. "62a. *C. glabriuscula* Sarg." = not certainly different from others with same number (e.g. 62, 62b, etc.). Sources: regional floras cited in text except for Mexico (Harvard University Herbaria), supplemented by a variety of local floras.

† = sample used in biogeographic analysis.

* = sample used in taxonomic studies.

Sect. Mexicanae Loud.

Ser. Mexicanae (Loud.) Rehd.

- †*1. *C. mexicana* Moc. & Sessé

Ser. 'Henryanae (Sarg.)'

- †*2. *C. scabrifolia* (Franch.) Rehd.

Sect. Oxyacanthae Loud.

Ser. Oxyacanthae (Loud.) Rehd.

- †*3. *C. monogyna* Jacq.
- *4. *C. curvisepala* Lindm. (= *C. calycina* auct. non Peterm.)
5. *C. macrocarpa* Hegetschw.
- *6. *C. kyrtostyla* Fingerh.
7. *C. turkestanica* Pojark.
8. *C. pseudoheterophylla* Pojark.
- *9. *C. laevigata* (Poir.) DC.
10. *C. turcomanica* Pojark.
11. *C. ambigua* C. A. Mey. ex Beck.
12. *C. volgensis* Pojark.
13. *C. transcaspica* Pojark.
14. *C. persica* Pojark.
15. *C. caucasica* C. Koch
- *16. *C. atrosanguinea* Pojark.
- *17. *C. songarica* C. Koch
18. *C. sphaenophylla* Pojark.
- *19. *C. microphylla* C. Koch
20. *C. stevenii* Pojark.
21. *C. beckeriana* Pojark. (= *C. pallasii* Griseb. in Fl. Eur.)
22. *C. ucrainica* Pojark.
- *23. *C. meyeri* Pojark. } series Erianthae
24. *C. eriantha* Pojark. } Pojark.
25. *C. taurica* Pojark. } ? → Azaroli
- (+ putative hybrids: *C. palmstruchii* Lindm., *C. leiomonogyna* Lkok., *C. heterodonta* Pojark., *C. poloniensis* Cin., *C. subbo-realis* Cin., *C. allemaniensis* Cin., *C. orientobaltica* Cin., *C. insularis* Cin.)

Ser. Apiifoliae (Loud.) Rehd.

- †*26. *C. marshallii* Egglest.

Ser. Pentagynae (Schneid.) Rus.

- *27. *C. pentagyna* Waldst. & Kit.
28. *C. davisii* Browicz (close to *C. pentagyna*—Fl. Turkey)
29. *C. pseudomelanocarpa* M. Pop. (eastern counterpart to *C. pentagyna*—Pojarkova)

Ser. Azaroli (Loud.) Rehd.

30. *C. pycnoloba* Boiss. & Heldr.
- *31. *C. orientalis* Pall.
32. *C. laciniata* Ucria
- *33. *C. tanacetifolia* (Lam.) Pers.
- *34. *C. azarolus* L. (incl. *C. aronia* (L.) Bosc.)
- *35. *C. pontica* C. Koch
36. *C. szovitsii* Pojark.
37. *C. sinaica* Boiss.
38. *C. dikmensis* Pojark.
- *39. *C. heildreichii* Boiss.

Sect. Sanguineae Zabel ex Schneid.

Ser. Pinnatifidae (Zabel ex Schneid.) Rehd.

- †*40. *C. pinnatifida* Bunge

Ser. Nigrae (Loud.) Rus.

- *41. *C. nigra* Waldst. & Kit.
42. Original is deleted from list.
- *43. *C. jozana* C. K. Schneid.

Ser. Sanguineae (Zabel ex Schneid.) Rehd.

- †*44. *C. sanguinea* Pall. ex Bieb.
- †*45. *C. dahurica* Koehne ex C. K. Schneid.
- †*46. *C. altaica* Lange
47. *C. wattiana* Hemsl. ex Lace (? = *C. korolkowii* Henry)

Ser. (un-named)

- †*48. *C. maximowiczii* C. K. Schneid.
- †49. *C. chlorosarca* Maxim.
- †*50. *C. kansuensis* Wils.
- †51. *C. chungtiensis* W. W. Smith
- 52. *C. aurantia* Pojark.
- 53. *C. remotilobata* H. Raik. ex Pop.

Ser. (un-named)

- *54. *C. clarkei* Hook. f.
- †*55. *C. wilsonii* Sarg.
- †56. *C. oresbia* W. W. Smith

Sect. (un-named)

- †*57. *C. hupehensis* Sarg.
- †58. *C. shensiensis* Pojark.

Sect. Cuneatae Rehd. ex Schneid.

- †*59. *C. cuneata* Sieb. & Zucc.
- *60. *C. tangchungchangii* Metcalf (?)

Sect. Cordatae Beadle ex Egglest.

- †*61. *C. phaenopyrum* (L. f.) Medic.

Sect. Virides Sarg. ex Schneid.

Ser. Virides (Sarg. ex Schneid.) Rehd.

- †*62. *C. viridis* L.
- 62a. *C. glabriuscula* Sarg.
- 62b. *C. sutherlandensis* Sarg.
- 62c. *C. anamesa* Sarg.
- 62d. *C. stenosepala* Sarg.
- 62e. *C. poliophylla* Sarg.
- †*63. *C. nitida* (Engelm.) Sarg.

Ser. Pulcherrimae (Sarg. ex Palmer) Palmer

- 64. *C. pulcherrima* Ashe

Sect. Microcarpae Loud.

- †*65. *C. spathulata* Michx.

Sect. Flavae Loud.

- †*66. *C. flava* Ait.
- 67. *C. aprica* Beadle
- 68. *C. michauxii* Pers.
- 69. *C. floridana* Sarg.
- 70. *C. lacrimata* Small

Sect. Parvifoliae Loud.

- †*71. *C. uniflora* Muenchh.

†Sect. Aestivales Sarg. ex Schneid.

- *72. *C. aestivalis* (Walt.) T. & G.
- 73. *C. opaca* Hook. & Arn.
- 74. *C. rufula* Sarg.
- 75. *C. maloides* Sarg. (incl. *C. fruticosa* Sarg., *C. luculenta* Sarg.)

Sect. Brevispinae Beadle ex Schneid.

- †*76. *C. brachyacantha* Engelm. & Sarg.

Sect. Douglasii Loud.

- †*77. *C. douglasii* Lindl.
- †*78. *C. rivularis* Nutt.
- 79. *C. erythropoda* Ashe (incl. *C. cerronis* Nels.)
- †80. *C. saligna* Greene (? correctly placed)

Sect. Crus-galli Loud.

Ser. Crus-galli (Loud.) Rehd.

- †*81. *C. crus-galli* L., sens. lat. (incl. *C. fontanesiana* Spach, *C. bushii* Sarg., *C. livoniana* Sarg., *C. pyracanthifolia* Beadle, etc., etc.)
- 81a. *C. reverchonii* Sarg.

- 81b. *C. cherokeensis* Sarg.

- 81c. *C. sublobulata* Sarg.

- 81d. *C. engelmannii* Sarg.

- †81e. *C. tracyi* Ashe

- 82. *C. berberifolia* T. & G.

- †83. *C. baroussana* Egglest. (?)

- †84. *C. parryana* Egglest. (?)

Ser. Punctatae (Loud.) Rehd.

- *††85. *C. punctata* Jacq.

- †85a. *C. collina* Chapm.

- †86. *C. brazoria* Sarg. (?)

- 87. *C. disperma* Ashe

Sect. Triflorae Beadle ex Schneid.

- †*88. *C. triflora* Chapm.

- 89. *C. austromontana* Beadle

- 90. *C. conjungens* Sarg.

Sect. 'Americanae (El-Gazaar)'

†Ser. Bracteatae (Palmer) Rehd.

- 91. *C. ashei* Beadle

- *92. *C. harbisonii* Beadle

- 93. *C. pearsonii* Ashe (?)

Ser. (un-named)

- †94. *C. viburnifolia* Sarg.

Ser. Molles (Sarg. ex Schneid.) Rehd.

- †*95. *C. mollis* (T. & G.) Scheele

- †95a. *C. noelensis* Sarg.

- 95b. *C. viburnifolia* Sarg.

- †95c. *C. texana* Buchel.

- †95d. *C. limaria* Sarg.

- 96. *C. canadensis* Sarg.

- 96a. *C. arnoldiana* Sarg.

- 96b. *C. anomala* Sarg.

- 97. *C. pensylvanica* Ashe

- †98. *C. greggiana* Egglest.

- †*99. *C. submollis* Sarg.

†*Ser. Coccineae (Loud.) Rehd.

- *100. *C. holmesiana* Ashe

- *101. *C. pedicellata* Sarg.

- *102. *C. pringlei* Sarg.

- 103. *C. acutiserrata* Kruschke

- 104. *C. fulleriana* Sarg.

- *105. *C. corusca* Sarg.

Ser. Tenuifoliae (Sarg. ex Egglest.) Rehd.

- †**106. *C. macrosperma* Ashe

- 107. *C. apiomorpha* Sarg.

- *108. *C. fluviatilis* Sarg.

- †*109. *C. schuettei* Ashe

- *110. *C. lucorum* Sarg.

- †*111. *C. flabellata* (Bosc.) K. Koch

Ser. Rotundifoliae (Egglest. ex Egglest.) Rehd.

- †112. *C. columbiana* Howell

- †*113. *C. chrysocarpa* Ashe

- †*114. *C. dodgei* Ashe

- *115. *C. flavida* Sarg.

- †116. *C. margaretta* Ashe

- 117. *C. irrasa* Sarg.

- 118. *C. aboriginum* Sarg.

- 119. *C. laurentiana* Sarg.

†Ser. Intricatae (Sarg. ex Schneid.) Rehd.

- *120. *C. intricata* Lange

- 121. *C. foetida* Ashe

Ser. Brainerdianae Palmer

- †*122. *C. brainerdii* Sarg.
123. *C. sylvestris* Sarg.
†*124. *C. scabrida* Sarg.
125. *C. coleae* Sarg.
*126. *C. jonesae* Sarg. (?)

Ser. Macracanthae (Loud.) Rehd.

- *127. *C. succulenta* Link
†*128. *C. macracantha* Lodd.
†*129. *C. calpodendron* (Ehrh.) Medic.

†Ser. Silvicolae (Palmer) Kruschke

- *130. *C. iracunda* Beadle
*131. *C. compacta* Sarg.
*132. *C. suborbiculata* Sarg.
133. *C. nitidula* Sarg.

134. *C. compta* Sarg.135. *C. prona* Sarg.136. *C. opulens* Sarg.137. *C. jesupii* Sarg.138. *C. beata* Sarg.139. *C. incerta* Sarg.

(? others)

Ser. Pruinosa (Sarg. ex Egglest.) Rehd.

- †***140. *C. pruinosa* (Wendl.) K. Koch, sens. lat.
141. *C. formosa* Sarg.
*142. *C. dissona* Sarg.

†Ser. Dilatatae (Sarg. ex Palmer) Rehd.

- *143. *C. dilatata* Sarg. (= *C. conspecta* Sarg.)
144. *C. coccinioides* Ashe
145. *C. glareosa* Ashe (?)